博士（地域研究）

学位申請論文

Plant Species Coexistence Controlled by Organic Matter Dynamics in the Tropical Peat Swamp Forest in Riau, East Sumatra, Indonesia

インドネシア、東部スマトラ、リアウ州の泥炭湿地林における
有機物動態が制御する植物種共存機構

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PLANT SPECIES COEXISTENCE CONTROLLED BY ORGANIC MATTER DYNAMICS IN THE TROPICAL PEAT SWAMP FOREST IN RIAU, EAST SUMATRA, INDONESIA

by

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Summary

In tropical peat swamp forests, the peat surface is characterized by considerable topographic heterogeneity at various scales, ranging from tens of centimeters to several meters. The large buttressed trees have a large amount of roots supporting the aboveground organs. The root architecture raises the peat surface around the buttresses and forms mounds. Some species have numerous pneumatophores that enable root respiration during flooding. Such species are found in non-mounds, while juveniles of other species are found on mounds.

In this thesis, I attempted to link plant community dynamics with the local scale of the organic matter cycle, associated with specific tree functions. To that end, this study evaluates how plant activities regulate peat surfaces and how the resulting conditions of peat surfaces affect plants, and, further, how such feedback between plant and soil contributes to species coexistence in a tropical peat swamp forest in Riau, East Sumatra.

I monitored the seedling demography of *Swintonia glauca* and *Stemonurus scorpioides*. *Swintonia glauca* seedlings had high survival rates in gaps and on mounds, and their mortality was negatively correlated with the distance from the nearest conspecific adult. *Stemonurus scorpioides* seedlings had high survival on non-mounded sites, and the morphology of *S. scorpioides* seedlings indicates that they are shade- and flood-tolerant.

The result of spatial point pattern analysis indicated that such different types of habitats regulate the regeneration process according to flood-tolerance of trees and contribute to species coexistence. For example, around the established buttressed trees there were fewer juveniles of flood-tolerant species and vice versa. Distribution of six species of the top ten most frequent tree species in terms of number of individuals in the forest indicate that their distribution is affected by microtopographic heterogeneity associated with their flood-tolerance. These results

suggest that the spatial distribution pattern was a consequence of a microtophographic interaction associated with the established buttressed and/or non-mound-forming trees, and that microtopographies contribute to species coexistence in this forest.

I studied the organic matter dynamics of different habitats. It was revealed that habitats are maintained by different regimes of production and decomposition, and changes in the balance between production and decomposition leads to the dynamics of microtopography. Death of buttressed trees causes the disappearance of mounds due to decreased organic matter productivity, and the establishment of large buttressed trees results in creation of mounds due to a high rate of production. The dynamics of microtopography explains the species coexistence along spatio-temporal scales. The creation and disappearance of mounds provide regeneration niches for flooding-intolerant and -tolerant species, respectively. I propose to call these mechanisms of habitat creation "elevation dynamics".

The elevation dynamics has several important implications. First, the dynamics modifies the effects of gap dynamics as a result of changes in the microtopographic form in gaps. Second, because the rise and sink of peat surfaces are associated with plant activity, the dynamics is an example of habitat modification of tree species. The finding of this dynamics constitutes the first observation of a demonstrated effect of habitat modification in tropical wet forests. Third, because a large amount of production of huge trees is common to other tropical rain forests and organic matter dynamics on the forest floor is affected by the amount of litter input, similar effects of huge trees may be present in other tropical forests.

Table of contents

List of tables

List of figures

List of plates

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CHAPTER 1

General introduction

1.1.Background and justification of the study

Plants provide a source of organic matter for soil, and decomposed organic matter releases nutrients for plant growth. Thus, above- and below-ground components of terrestrial ecosystems are co-dependent. The interactions at the interface of above- and below-ground may provide important feedback regulating ecosystem processes. Such effects of plants on nutrient cycling have attracted considerable interest in individual species at the level of functional groups (Bardgett et al. 1998, Hooper and Vitousek 1998, Wardle et al. 1999, Prescott 2002, Quested et al. 2002) and/or the plant community level (Naeem et al. 1995, Tilman et al. 1996, Porazinska et al. 2003). In addition, the effects of such plant species on nutrient cycling can constitute feedback to the plant community, and often such effects serve to facilitate other individuals by providing preferable habitat conditions (Franco and Novel 1989, Challaway 1994, Pugnaire et al. 1996, Pugnaire and Luque 2001, Quested et al 2003, Tirado and Pugnaire 2003).

Most studies that have dealt with such habitat modification via soil processes mainly focus on very few species and the relationships among shrubs and/ or herbaceous plants. Compared to shrubs and herbaceous plants, large trees spread a broad amount of roots around them and have large crowns consisting of leaves and twigs. If such large trees exert effects of habitat modification, they affect a larger modified area per individual than do shrubs and herbs. Compared to the respective lifespans of shrubs and herbs, that of such large trees is much longer. Eccles (1999) suggested that the effects of plants on habitat modification are likely to be stronger when they grow over a long period of time. Thus, the effects of habitat modifications of

such large individuals as trees may be stronger than those of other plants. The modified condition of surrounding environments strongly depends on each individual. The death of such an individual results in creation of a gap that causes changes in the environment. Thus, a complex mosaic of modified, non-modified, and post modified environmental conditions creates environmental heterogeneity, of which various effects on the plant community can be assumed. However, the effects of habitat modification of such large individuals are not well known. Such facilitative effects have been often documented at harsh sites such as salt marshes (Callaway 1994, Bruno and Kennedy 2000), arctic regions (Walker and Chapin 1986, Chapin et al. 1994, Carlsson and Callaghan 1996, Quested et al. 2003) semi-arid environments (Pugnaire et al. 1996, Tirado and Pugnaire 2003), and deserts (Franco and Novel 1989, Forseth et al. 2001), because environmental modification is more important for plants at sites where environmental stress is relatively high (Pugnaire and Luque 2001). Stressful environments impede the occurrence of large trees. Thus, it is difficult to detect the effects of large trees on plant communities with high species diversity, despite the fact that they are assumed to have an important effect. Here, the objective was to reveal the role of large plants on the plant community via soil processes.

1.2. Objective of the study

In a peat swamp forest in Riau, East Sumatra, the surface topography is undulating and has many mounds around the base of each tree trunk. Especially around huge buttressed trees (they form an emergent layer), large mounds are found. Root architecture supporting the aboveground organs raises the ground surface around buttresses. On the other hand, some species that include numerous pneumatophores are found in non-mounds. Therefore, a complex mosaic of undulating peat surface results in heterogenous conditions on the forest floor. While non-mounds are inundated, mounds avoid inundation. Such complex microtopographic

heterogeneity of the peat surface is also recognized on the Malay peninsula (Yonebayashi et al. 1997) and in Borneo (Page et al. 1999) and Sumatra (Brady 1997).

A tropical peat swamp forest presents an appropriate ecosystem for studying plant species interaction through soil processes for three reasons. First, plant activities regulate the conditions of the peat surface (mound or non-mound) on a small scale. Peat that supports the terrestrial ecosystem is originated from plant materials. The balance between production and decomposition ultimately regulates the accumulation and maintenance of peat as it does of boreal peat (Wieder and Lang 1983). The surface peat materials are modern age (post 1950 AD) (Maloney and McComac 1995, Brady 1997), and peat surface properties are vulnerable to organic matter input and decomposition. Thus, organic matter dynamics at the local level determines the status of peat surface; i.e, the presence of mounds and non-mounds. Where production exceeds decomposition, the peat surface may rise and a mound will be created. Where the rate of decomposition exceeds production, the peat surface may sink. The mass of production is due mainly to the activity of a large individual on a small-scale level. Large individuals determine the condition of the peat surface (mound or non-mound) at the local level. Here we can assume the spatial association between specific mirotopography and large individuals of specific trees. For example, a huge buttressed tree spreads a mounded site around itself, while an individual without buttresses does not spread mounds around its site. Such difference in microtopography is due to differences in the regime of production and decomposition.

Second, in wetlands, the relative position of the soil surface and the water table strongly regulate the distribution of plants (Keddy 1983, Huenneke and Sharitz 1986, Denneler et al. 1999, Catelli et al. 2000), seedling survival (Budelsky 2000), and seedling germination (Seabloom 1998, Smith 1995). In tropical heath forests, Miyamoto et al. (2003) pointed out that

humus depth contributes to spatial distribution of plant species on a small scale. Therefore, established individuals that are associated with specific microtopography in tropical peat swamp forests affect younger individuals by modifying the condition of peat surface, which may determine plant distribution.

Third, effects of habitat modification in harsh sites (Callaway 1994, Forseth et al. 2001, Quested et al. 2003) have been often documented, reflecting the fact that such environmental modification is more important for plants as environmental stress increases (Pugnaire & Luque 2001). Tropical peat is characterized by a low nutrient content and high acidity, and the peat surface is seasonally inundated. Thus, tropical peat swamp forests provide harsh environments for plants. It is expected that effects of habitat modification are important in this ecosystem.

Therefore, tropical peat swamp forest is one of the ideal ecosystems for studying plant interaction via soil processes. There are over one hundred tree species within 0.6 ha (Momose and Shimamura 2002). The canopy of some trees compose the emergent stratum. As already mentioned above, the effect of large plants on a diverse community is not well known, though large plants can be assumed to have important effects. The objective of this study is to reveal the role the effects of large plants play in the plant community via soil processes in a tropical peat swamp forest. To this end, I focused on large individuals among the established buttressed trees, because they spread mounded sites around them, and mounded sites may have important effects on the plant community.

1.3. Hypotheses of the study

In tropical peat swamp forests, mounds around large buttressed trees constitute a remarkable microtopographic form. Suppose that a large buttressed tree falls down. Subsequently, the roots that raised the ground surface are decomposed, and the mound becomes lower and finally disappears. Non-mound sites are frequently inundated, and are dominated by flood-tolerant

species. By contrast, the development of large buttresses forms mounds that less water-tolerant species can inhabit. I hypothesized that this cyclic rising and sinking of the ground surface contributes to species coexistence in the tropical peat swamp forest by providing an axis of habitat partitioning. Consequently, the cyclic rising and sinking of the ground surface explains species coexistence in kinetic equilibrium along the spatiotemporal scale.

To test this hypothesis, I developed the two general hypotheses of the present thesis. First, microtopographic heterogeneity provides an axis of habitat partitioning. If this hypothesis is true, the spatial aspects of a species coexistence mechanism will be supported. I described the regeneration of seedlings (Chapter 3), spatial association of tree species between large trees that are associated with mounded or non-mounded sites and dominant tree species (Chapter 4). Second, rising and sinking of the peat surface occurs in the peat swamp forest. If the second hypothesis is true, the temporal aspects of a species coexistence mechanism will be supported. The dynamics of the peat surface is determined by accumulation and decomposition of organic matter. Thus, I described the organic matter dynamics that is associated with specific microtopographic forms (Chapter 5).

Plate 1-1. An established buttressed trees of *Swintonia glauca*

CHAPTER 2

Study site

2.1. Study site

This study was conducted in the tropical peat swamp forest in Kermutan Wildlife Sanctuary, Riau Province, Eastern Sumatra, Indonesia (Figure 2-1). The Kermutan River, a branch of the Kampar River, forms the northern boundary of the Kermutan Wildlife Sanctuary. The research plot is located 800 m inland from the riverbank and 0° 7′ N, 102° 28′ E. According to the local people and our observation around the research site, illegal commercial logging by local people began in 1991, though the logging has not yet invaded the area of protected forests. A small amount of timber was logged for self-consumption before 1991. It has been difficult and non-profitable for local people to bring logged timber for self-consumption ca. 800 m inland from the riverbank. According to the local people, logging had occurred at our research site. The site can be regarded as virgin forest.

I laid out study plots ca. 800m - 1 km inland from the Kermutan River. Bores indicated that the peat depth was ca. 4 - 5 m in the study plots. The type of the forest is similar to what we call mixed swamp forest (Anderson 1961, Page et al. 1999). In the study plot, over 110 tree species exceeding 1 cm in diameter at breast high were found (Momose and Shimamura 2002). The dominant emergent trees are *Swintonia glauca* Engl. (Anacardiaceae), *Shorea teysmanniana* Dyer, ex Brandis (Dipterocarpaceae), and *Tetramerista glabra* Miq. (Tetrameristaceae) (Table 2-1).

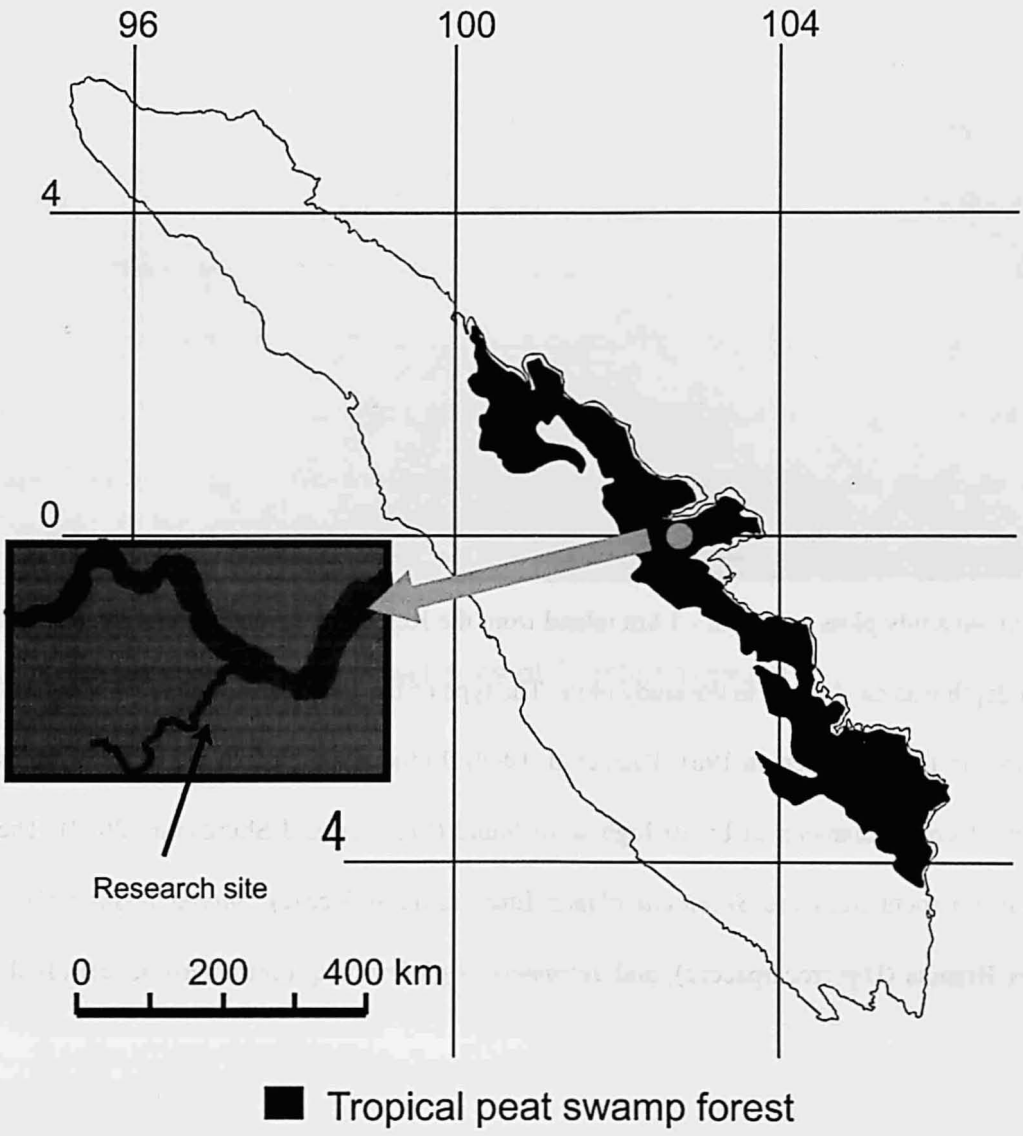

Figure 2-1. Location of study site and distribution of tropical peat swamp forest of Sumatra.

2.2. Climate

The climate of Sumatra exhibits great variation, mainly with regard to rainfall. The east coast of the island has a wet tropical monsoon climate classed by the Köppen System as "Af". Fontanel and Chantefort (1978) characterized the coast as having a very humic bioclimate with 2000-2500 mm annual rainfall, with no dry season, and a mean temperature in the coldest month of greater than 20 °C (cited in Brady 1997).

Precipitation was monitored between September 2000 and July 2002, using a tipping-bucket rain gauge located at our research station about 5 km away from the study site. Annual precipitation was 1,906 mm in 2001 and 1,752 mm in 2002. Mean (SD) monthly precipitation during the monitoring period was 149 mm (11.4). Maximum and minimum monthly precipitations during the monitoring were 305 mm in October 2001 and 27.0 mm in July 2001, respectively. The mean values of annual precipitation were lower than that in 2000, based on data of the east coast of Sumatra gathered by Fontanel and Chantefort (1978).

When the water table is high, the forest floor is patchily inundated, especially in the rainy season. Mean (SD) daily height of the water table was -30.3 cm (1.24). Maximum and minimum daily height of the water table were 18.7 cm on 14th December 2001 and -87.1 cm on 20th August 2001, respectively.

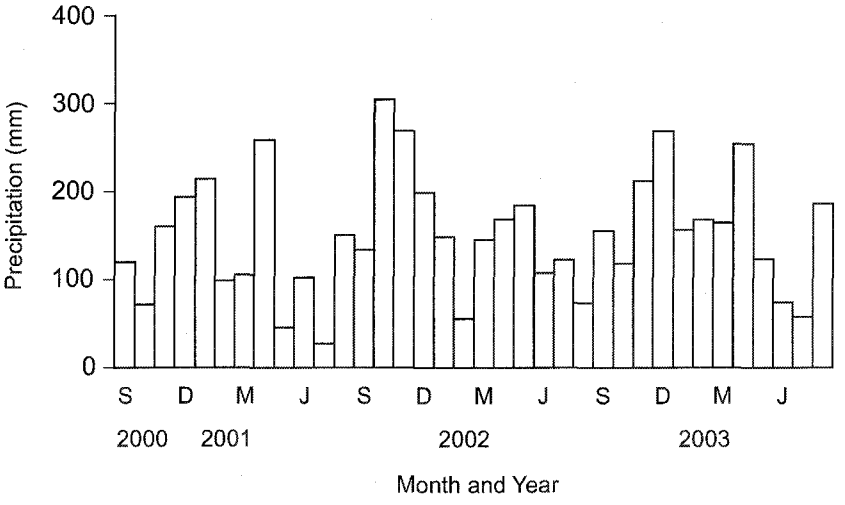

Figure 2-2. Monthly precipitation obtained near the study plot from August 2000 to August 2003.

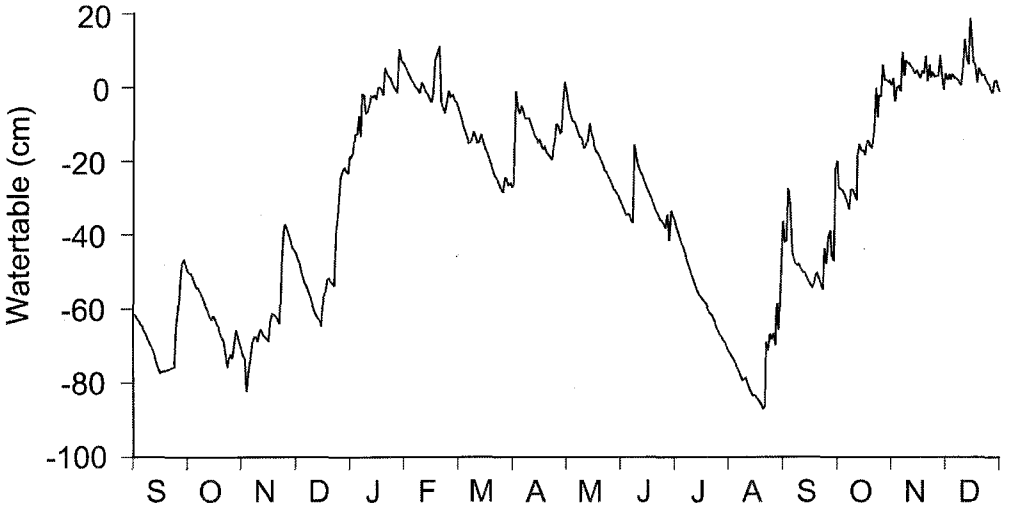

Figure 2-3. Hydrograph of ground water table obtained near the study plot from August 2000 to December 2001.

CHAPTER 3

Seedling regeneration

3.1. Introduction

Habitat heterogeneity affects the distribution and components of species (Austin et al. 1996). Since germination and seedling establishment are the most vulnerable stages in plant life-cycles (Solbrig et al. 1980), studies of demographic variation in these stages are indispensable to understanding the regeneration niches (Grubb 1976) of species. In wetlands, the distributions of adults are mainly affected by water depth (Castelli et al. 2000). However, attempts to explain the distribution of wetland plants based solely on the response of adults to water depth have been unsuccessful in most cases (de Swart et al. 1994). This suggests that other factors (e.g., regeneration niches) are important in determining the distribution of adult trees. Consequently, many authors have studied seed and seedling stages in wetlands (Nicholson & Keddy 1983; Streng et al. 1989; Smith et al. 1995; Seabloom et al. 1998; Minchinton 2001).

Microtopography (topographic patterns at the scale of individual plants) creates a complex mosaic of microsites that differ in structural, hydrological, and chemical features (Robertson et al. 1978; Hackney et al. 1996; Bledsoe & Shear 2000). Small differences in the depth of the water table result in significant differences in herbaceous and woody vegetation. Direct gradient analyses of vegetation along elevation gradients in floodplains and other wetland areas have demonstrated that individual plants respond to flooding intensity. The effects of static (not kinetic) elevation status explain vegetative zonation, but do not explain species coexistence within the same plant community.

As indicated in Chapter 1, mounds around large buttresses constitute a remarkable microtopographic form in the tropical peat swamp forest. In this section, I evaluated the effects

of microtopographic heterogeneity on seedling regeneration process, as compared with the effects predicted from the gap dynamics (Whitmore 1989) and Janzen-Connell hypotheses (Janzen 1970, Connell 1971) that are well-known explanations for species coexistence. For this purpose, the regeneration processes of seedlings were described, and mounded sites that spread around large buttresses as a remarkable microtopography were focused on.

3.2. Materials and methods

Species Studied

Swintonia glauca Engl. (Anacardiaceae) is native to East Sumatra and Borneo, and is distributed mainly in peat swamp forests and lowland dipterocarp forests. It produces one seeded ellipsoid drupes 1.75-2.5 cm in length and 0.75-1.5 cm in diameter (Ding Hou 1978). Mature trees reach the emergent layer, and develop large buttresses; DBH can reach 70 cm. Seedlings are of the phanero-hypogeal-reserve type (sensu Garwood 1996).

Stemonurus scorpioides Becc. (Icacinaceae) is found in *Shorea albida* peat swamp forests in Borneo and in seasonal swamp forests on peaty or sandy soils. It produces one seeded ovoid-ellipsoid drupes 4.5-5.5 cm in length and 2.0-2.5 cm in diameter (Sleumer 1971). At the study site, mature trees (approximately 40 cm DBH) are components of the forest canopy and have stick-like pneumatophores. Seedlings are of the phanero-epigeal-foliaceous type (sensu Garwood 1996).

Plot Design

To reveal factors affecting the regeneration process, I laid out two plots, ca. 10 m apart, where seedlings of the studied species were abundant, as to include various habitat conditions. One of the plots was dominated by *Swintonia glauca* (plot SW) and the other was dominated by

Stemonurus scorpioides (plot ST). Each plot was divided into 1.5 × 1.5 m quadrats. Plot SW had 160 quadrats (total 360 m^2); 24 (54 m^2) of these were located in a gap and I refer to them as the gap plot. The remaining quadrats of plot SW were in the understory and I refer to them as the understory plot. Plot ST contained 12 quadrats (27 m^2) and all of them were located in the understory. In and around SW and ST plots I measured DBHs (for individuals that has swelling at breast height, diameter at above the swelling was measured) and locations of trees (DBH ≥ 10 cm). Nine individuals of *Swintonia glauca* and six individuals of *Stemonurus scorpioides*, were recorded (Figure 3-1). All of these trees (dbh ≥ 10 cm) fruited in February – March 2000. Thus, in this paper, I call them adult trees.

In plots ST and SW, the demography of seedlings of the two study species that emerged between March 2000 and 24 June 2001 was monitored. All these seedlings were tagged. Seedling survival was monitored twice weekly from March to June, weekly in July, biweekly in August, and monthly from September to the following June. The existence of leaves on each individual was also checked.

Seedling Death

For *Swintonia glauca*, the causes of seedling mortality during the first three months of the census were classified into four categories: (1) herbivory, (2) damping off, (3) physical damage, and (4) others or undefined. Seedlings that died with symptoms such as sudden silting of leaves, softening of hypocotyls, or toppling of the stem were diagnosed with damping off. Seedlings in which the hypocotyls or most of the leaves were eaten, absorbed, or cut were recorded as herbivory. Hemipteran nymphs were prominent herbivores. Dead seedlings with broken or bent stems were recorded as physical damage.

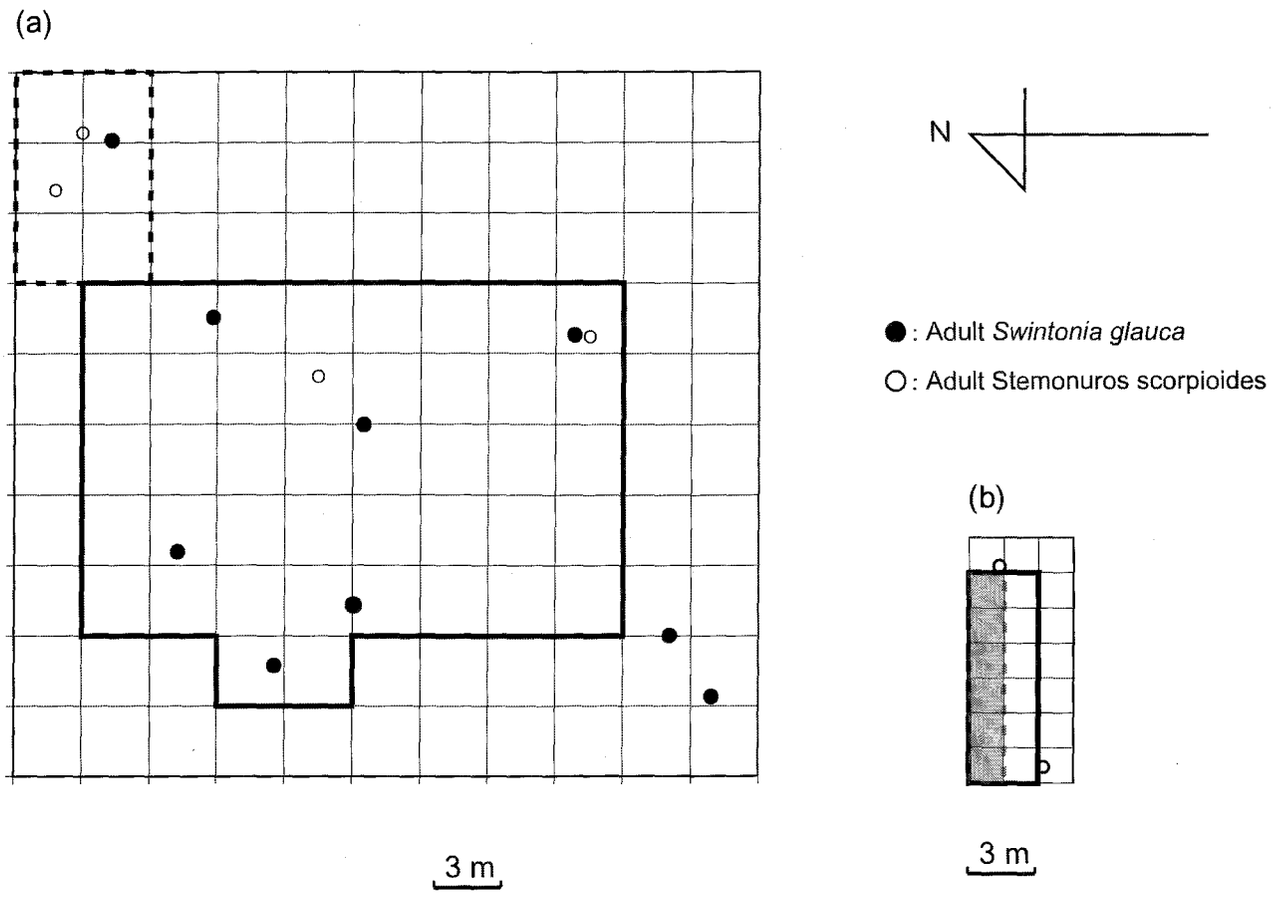

Figure 3-1. Maps of plots SW (a) and ST (b). In plot SW, the area circumscribed by the solid line is the understory plot and the area circumscribed by the dotted line is the gap plot. In plot ST, seedlings were harvested from the shaded areas.

Harvest and Allocation

On 24 June 2001, the day of the last census, all the tagged seedlings in plot SW and in six quadrats in plot ST were harvested (Figure 3-1). These seedlings were separated into leaves, stems, and roots. The lengths of the stems and taproots were measured. Leaves were pressed and dried to preserve them. Using pressed leaves, leaf areas were measured with a leaf-area meter (AAM-8, Hayashi Denko, Tokyo, Japan). After these measurements, all plant materials were dried to a constant mass in a forced-air oven at 80°C and weighed.

Environmental Factors

The physical and biological environments of every quadrat in plots ST and SW were surveyed. For physical environments, I estimated direct light (DSF; direct site factor), diffused light (ISF; indirect site factor) and elevation. For the biological environment, I measured the distance from the nearest conspecific adult tree.

To estimate the light level, hemispherical canopy photographs were taken in the center of each 1.5 × 1.5 m quadrat in plots ST and SW at a height of 1.0 m above the ground with a fish-eye camera (Cool Pix 900 with Fish-eye converter FC-E8, Nikon, Tokyo, Japan), in March 2001. The images were processed using a program software (Hemiview, Delta-T device Ltd. Cambridge, UK) to calculate indirect site factor (ISF) and direct site factor (DSF). ISF represents the proportion of diffuse photosynthetic photon flux density (PPFD) incident on a horizontal surface above the canopy that is transmitted to the point where the photograph is taken, and is calculated by assessing the proportion of pixels classified as sky within the projected image of the hemisphere. DSF represents the proportion of PPFD transmitted to the point of the photograph relative to that outside the canopy determined by the sun track, and is estimated by imposing solar tracks on the digitized image, enabling the proportion of open

pixels to be calculated. Indirect estimation from hemispherical photography gives a reliable ranking of PPFD and its relative difference among the sites (Engelbrecht and Herz 2001). Then, Site Factors are used as indices of light condition among quadrats.

In the present thesis, elevation is defined as the distance between the ground surface and the water table on 14 February 2001, middle of the rainy season when the water table was high. To study the relationship between seedling performance and water table, small holes were dug, and the elevation were measured at each corner of quadrats in plots ST and SW. The elevation of each quadrat in plots ST and SW was given by the average of the four corners of the quadrat.

Analysis

To reveal factors affecting seedling survival, I conducted quadrat-based analysis. I determined the survival ratio (SR) of seedlings, as a dependent variable in the multiple regression model. This variable was defined as the ratio of the number of seedlings surviving until 24 June 2001 to the number of seedlings that emerged in each 1.5 × 1.5 m quadrat in 2000. Quadrats with less than six seedlings that emerged were excluded from the multiple regression analysis of SR because the value of small numbers varies greatly by chance. Five factors were considered independent variables: DSF, ISF, number of emerged seedlings per quadrat (DENS), distance from the nearest conspecific adult tree (DIST), and elevation (ELEV). The number of emerged seedlings was log transformed, since its distribution was closer to log normal than to normal.

In the multiple regression analysis, significant independent variables were selected by backward elimination. If the multiple regression model was not significant in an analysis of variance, the factor with the lowest F value was removed, and the regression was repeated. This procedure was continued until all remaining independent variables were significant.

From the harvest data, the following variables were derived as dependent variables for the multiple regression analysis: stem mass ratio (stem mass/total plant mass, in g g^{-1}), leaf mass ratio (leaf mass/total plant mass, in g g^{-1}), root mass ratio (root mass/total plant mass, in g g^{-1}), specific leaf area (leaf area/leaf mass, in cm^2 g^{-1}), leaf area ratio (leaf area/total plant mass, in cm^2 g^{-1}), leaf area root mass ratio (total leaf area/root mass, in cm^2 g^{-1}), specific stem length (stem length/stem mass, in cm g^{-1}), specific tap root length (tap root length/root mass, in cm g^{-1}), and ratio of stem length to tap root length (stem length/tap root length, in cm cm^{-1}). These variables were log transformed, since their distributions were closer to log normal than to normal. In addition to DIST, ELEV, DSF, and ISF, surviving seedling number and biomass (biomass of each individual, in g) (log transformed) were used as dependent variables. Since it is difficult to separate the effects of environmental factors and plant sizes, biomass was added as a dependent variable (see Poorter 1999). Further procedure was the same as multiple regression analysis on SR.

3.3 Results

Environmental Factors

The topography around adult trees of *Swintonia glauca* and *Stemonurus scorpioides* in plots SW and ST were different (Figure 3-2). Elevation gradually decreased with increasing distance to the nearest adult of *Swintonia glauca*, whereas the elevation around adults of *Stemonurus scorpioides* was concave. Adult trees of *Swintonia glauca* have buttresses, and those of *Stemonurus scorpioides* have not (see Species Studied). Thus, this result was consistent with the measurement of mounds around large buttressed trees.

Indirect Site Factor and DSF decreased with distance from adults of *S. scorpioides*. The change in DSF with the distance from adults of *Swintonia glauca* was not significant, while ISF

was negatively regressed (Figure 3-2).

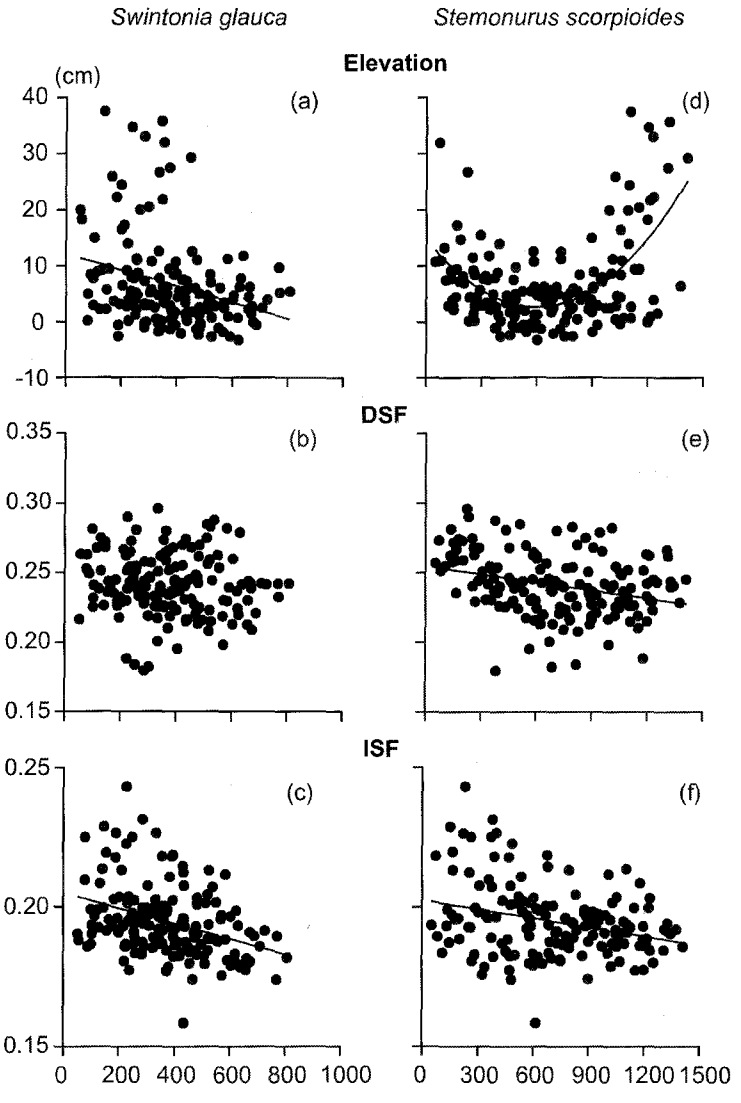

Figure 3-2. Relationships between distance from the nearest adult and the environment (elevation, Direct Site Factor (DSF), and Indirect Site Factor (ISF)) in plots SW and ST. Regression lines are shown when the regression was significant ($p<0.05$). For graph (d), I used a quadratic regression because the distribution was concave. Data for elevation was measured at each lattice point of the quadrats. Data for ISF and DSF were obtained from the center of each quadrat.

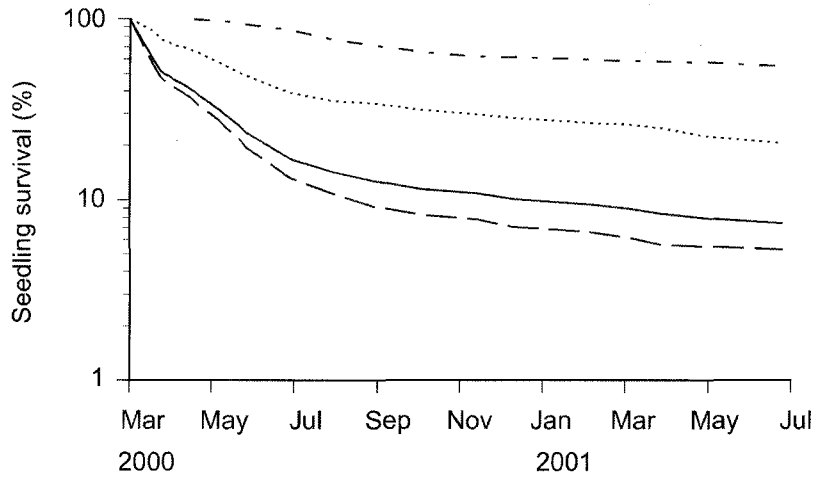

Figure 3-3. Survivorship of seedlings of *Stemonurus scorpioides* (dotted and broken line) and those of *Swintonia glauca* (solid line). In the case of *Swintonia glauca*, survivorship of seedlings was separately obtained for the gap (dotted line) and understory (broken line) plots.

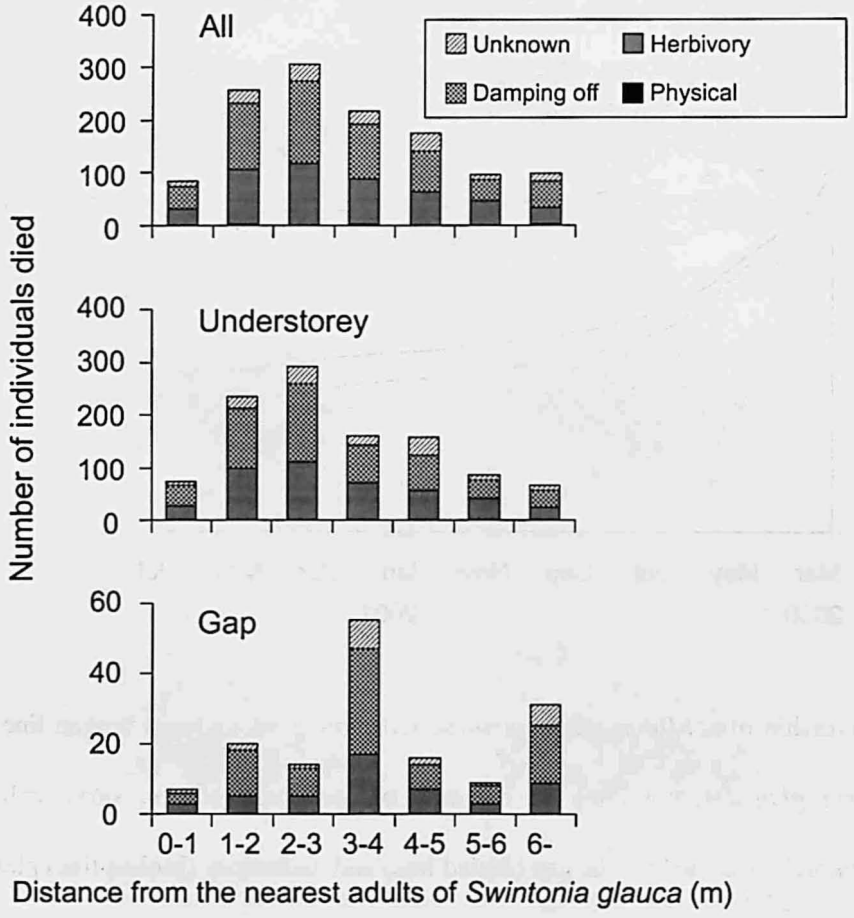

Figure 3-4. Changes in mortality factors affecting *Swintonia glauca* with distance from the nearest conspecific adult.

Table 3-1. Factors affecting the seedling survival ratios of *Swintonia glauca* and *Stemonurus scorpioides* in the multiple regression model. The result for *Swintonia glauca* in the gap is not shown because it was not significant.

	Swintonia glauca				*Stemonurus scorpioides*	
	All		Understory			
Factors	Effect	*F*	Effect	*F*	Effect	*F*
First density (log scale)	···	···	···	···	···	···
Indirect Site Factor	-	6.20**	···	···	-	17.4***
Direct Site Factor	+	7.00**	···	···	···	···
Distance from the nearest conspecific adult	···	···	+	6.35**	···	···
Elevation	···	···	+	5.92*	-	5.63*
Analysis of variance of model (d.f.)	···	5.55**(2,101)	···	5.13**(2,79)	···	8.77**(2,14)
Fitness of model	···	0.0990	···	0.115	···	0.556

*$p < 0.05$, **$p < 0.01$, *** $p < 0.001$

Factors Affecting Seedling Survival

Germination of *S. glauca* started at the beginning of March 2000, and continued until the end of July 2000. Therefore, by the start of this study, some *S. glauca* seeds had already germinated and died. The living and dead stems of seedlings (n = 1652) that appeared to have germinated within the previous a few weeks were tagged to determine the SR for *S. glauca* and recorded their survivorship (Figure 3-3). For *S. glauca*, the most severe mortality was observed within two months after germination; more than half of the *S. glauca* seedlings died before the end of June. The SR of *S. glauca* differed significantly between gap and understory (26.4% $year^{-1}$ in the gap plot, 6.7% $year^{-1}$ in the understory plot: $\chi^2 = 60.0$, $p < 0.0001$ and 9.49% $year^{-1}$ for the entire plot) (Figure 3-3).

Germination of *Stemonurus scorpioides* began in the middle of April 2000 and ended by the end of July 2000. This period was shorter than the germination period of *Swintonia glauca*. At the end of the census, 14 months after the beginning of germination, 55% (= 65.8% $year^{-1}$) of *Stemonurus scorpioides* seedlings survived (Figure 3-3). They succeeded in forming a seedling bank.

The causes of seedling mortality in *Swintonia glauca* were determined only in the first three months. Damping off was the predominant cause (Figure 3-4) and accounted for 68% of seedling deaths in the entire plot (plot SW) and 69% in the understory plot. There were no significant correlations between DIST and the percentages of herbivory or damping off in the entire plot or gap and understory plots (the correlation coefficients ranged from 0.16 to 0.033: n.s.), when the quadrats containing more than five seedlings were analyzed.

The results of the multiple regression analysis indicated that light environment was important for survival in both species (Table 3-1). While ISF had a negative effect on the SR of

S. glauca, DSF had a positive effect. This difference in light environments was not caused by multicollinearity, because their correlation was low (r = 0.19, n.s.) (see Discussion). Survival ratio of *S. glauca* in the gap plot was not significantly correlated with any factors. Elevation and DIST had positive effects on the SR of *S. glauca* in the understory plot. As the most remarkable result, ELEV had opposite effects on the SR of *S. glauca* in the understory plot (positive) and that of *Stemonurus scorpioides* (negative).

Table 3-2. Results of *t* tests for differences in allocation or morphology associated variables between seedlings of *Swintonia glauca* and *Stemonurus scropioides*. The variables were log transformed, except for leaf number. The back-transformed logarithmic means are shown, except for leaf number.

Variable	*t*	*Swintonia glauca*	*Stemonurus scorpioides*
Sample number		115	263
Biomass (g)	6.45***	1.15	0.720
Leaf mass ratio	4.02***	0.256	0.205
Stem mass ratio	-3.54***	0.384	0.423
Root mass ratio	-5.08	0.320	0.376
Specific stem length (cm/g)	1.96	51.7	47.2
Specific tap root length (cm/g)	0.375	51.5	50.4
Total leaf area/root mass (cm2/g)	4.62***	101	72.0
Leaf area ratio (cm2/g)	4.75***	32.8	25.3
Mean leaf area (cm2)	2.55**	12.9	11.0
Stem length/tap root length	2.19*	1.18	1.05
specific leaf area (cm2/g)	1.55	128	121
Leaf number	8.15***	3.28	1.69

*$p < 0.05$, **$p < 0.01$, *** $p < 0.001$

Allocation and Morphology

Compared with *S. scorpioides* seedlings, *Swintonia glauca* seedlings had a higher biomass. It is apparent that leaf-associated variables of *S. glauca* were explicitly higher than those of *Stemonurus scorpioides* (Table 3-2). Both species reinforced their roots and stems and increased leaf area and specific leaf area according to biomass (Tables 3-3 and 3-4). The allocation-associated variables (stem mass ratio, leaf mass ratio, and root mass ratio) of *S. scorpioides* were affected by biomass, while those of *Swintonia glauca* were not. Among the variables that were significantly correlated with biomass, biomass had the highest F value for both species. *Stemonurus scorpioides* reinforced their axes and decreased leaf-associated variables along the gradient of DSF, while ISF showed the opposite effect to a degree. Higher ISF enhanced leaf-associated variables of *Swintonia glauca* and decreased its allocation to roots. In *Stemonurus scorpioides*, the ratio of root length to stem length reduced with ELEV. The biological environment (DIST or DENS) enhanced the allocation to stems in both species.

Table 3-3. Factors affecting morphology and allocation of *Swintonia glauca* in the multiple regression model.

	Stem mass ratio		Leaf mass ratio		Root mass ratio		Specific leaf area		Specific stem length	
	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*
Biomass	···	···	···	···	···	···	-	19.6***	-	173***
Indirect Site Factor	···	···	+	5.82*	-	5.11*	···	···	···	···
Distance from the nearest conspecific adult	+	7.56**	···	···	···	···	···	···	···	···
Analysis of variance of model	···	7.56**	···	5.82*	···	5.11*	···	19.6***	···	173***
Fitness of model	···	0.063	···	0.0498	···	0.0436	···	0.150	···	0.607

	Specific tap root length		Leaf area ratio		Mean leaf area		Leaf area/root mass	
	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*
Biomass	-	81.6***	-	5.05*	+	75.5***	···	···
Indirect Site Factor	···	···	···	···	+	11.8***	+	6.21*
Elevation	···	···	···	···	+	7.09**	···	···
Analysis of variance of model	···	81.6***	···	5.05*	···	6.21***	···	6.21*
Fitness of model	···	0.426	···	0.0435	···	0.464	···	0.0534

*$p < 0.05$, **$p < 0.01$, *** $p < 0.001$

Table 3-4. Factors affecting morphology and allocation of *Stemonurus scorpioides* in the multiple regeresion model.

	Stem mass ratio		Leaf mass ratio		Root mass ratio		Specific stem length		Specific tap root length	
	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*
Biomass	-	56.5***	+	80.3***	-	47.1***	-	162***	-	43.7***
Density	+	20.3***	···	···	···	···	···	···	···	···
Direct Site Factor	···	···	-	17.0***	+	8.10**	-	14.3***	-	14.3***
Indirect Site Factor	···	···	···	···	···	···	+	14.8***	+	16.4***
Analysis of variance of model	···	32.8***	···	42.4***	···	25.2***	···	68.7***	···	25.9***
Fitness of model	···	0.203	···	0.291	···	0.165	···	0.444	···	0.234

	Stem length/root length		Leaf area/root mass		Leaf area rato		Mean leaf area		Specific leaf area	
	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*	Effect	*F*
Biomass	···	···	+	57.6***	+	81.3***	+	309	-	12.1
Density	···	···	-	6.54*	···	···	···	···	···	···
Direct Site Factor	···	···	-	10.5**	-	36.3**	···	···	···	···
Indirect Site Factor	···	···	···	···	+	19.7*	···	···	···	···
Elevation	-	7.98**	···	···	+	3.95	···	···	···	···
Analuysis of variance of model	···	7.98**	···	21.8***	···	5.37**	···	309***	···	12.1***
Fitness of model	···	0.0300	···	0.245	···	0.0503	···	0.603	···	0.056

*$p < 0.05$, **$p < 0.01$, *** $p < 0.001$

3.4. Discussion

The low SR of *Swintonia glauca* in the understory plot, compared with that for the gap plot and *Stemonurus scorpioides* indicates that *Swintonia glauca* is a shade-intolerant species. The high SR in the gap plot indicates that the light environment is an important factor for maintaining the first-year seedling population of this species. Although there were no data for gaps (actually, seedlings were hardly found in gaps due to limited dispersal ability of fruits), the high SR of *Stemonurus scorpioides* in the understory indicates that this species is shade-tolerant.

In this study, DSF and ISF had opposite effects on the SR of *Swintonia glauca* (Table 3-1). There was no significant correlation between DSF and ISF in plot SW. Indirect Site Factor was higher in the understory plot than in the gap plot, while DSF was higher in the gap plot. A sparse canopy covered the understory plot, and the hemispherical photograph of the gap plot shows an opening surrounded by a dense canopy (Figure 3-5). The existence of obstructions immediately above the forest floor strongly affected DSF at a given location, while values of ISF were equally affected by the proportion of obstructions in hemispherical photographs. Therefore, DSF was higher in the gap plot than in the understory plot due to the opening right above the gap plot. ISF was lower in the gap plot than in the understory plot because dense canopy surrounding the gap.

In wetland tree communities, the flood tolerance of seedlings differs among species (Keddy & Ellis 1985). The survival of seedlings of *S. glauca* in the understory plot was positively regressed with ELEV, while the regression for *Stemonurus scorpioides* was negative (Table 2-1). Therefore, *Swintonia glauca* is a flood-intolerant species and *Stemonurus scorpioides* is a flood-tolerant species. However, the regression analysis indicates that there was no significant regression between ELEV and the survival of *Swintonia glauca* when the survival of the gap plot was considered. Then, the light environment is the most important factor affecting the

survival of *S. glauca* at this very young stage, and elevation is a secondary factor.

Negative distance dependent mortality (Table 3-1) was found for seedlings of *S. glauca* in the understory. The result supports the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), which states that seedlings aggregated around parent trees are subjected to distance- or density-dependent mortality. The hypothesis often supported in tropical non-swamp forests (Clark & Clark 1984; Nichols et al. 1999), wetlands (Streng et al. 1989), and peat swamp forests (Gavin & Peart 1997). Low light conditions, competition due to dense seedling populations, litter fall (Clark & Clark 1984), herbivores (Clark & Clark 1984; Thomas 1990), and pathogenic fungi (Augspurger 1983, 1984b; Wills et al. 1997) have been suggested as causal agents for poor survival near parent trees.

In this study, differences in the rates of herbivory and damping off were not related to DIST. Two other possible causes of higher seedling mortality near conspecific adults are low light or high competition due to dense seedling populations (Clark & Clark 1984).

It is difficult to work out how the low light environment near large trees explains the distant-dependent mortality of *S. glauca*, because ISF was high near the large trees and DSF did not show any trend along the gradient. The SR of *S. glauca* was not significantly regressed with conspecific seedling density (Table 2-1). Far from it, there was negative evidence that there is competition among dense seedling population. Their biomass showed positive correlation to surviving seedling density ($r = 0.249$, $p < 0.01$: both variables were log transformed). In summary, mortality in *S. glauca* depends on distance, but this phenomenon does not seem to be caused by any single factor that has been proposed previously.

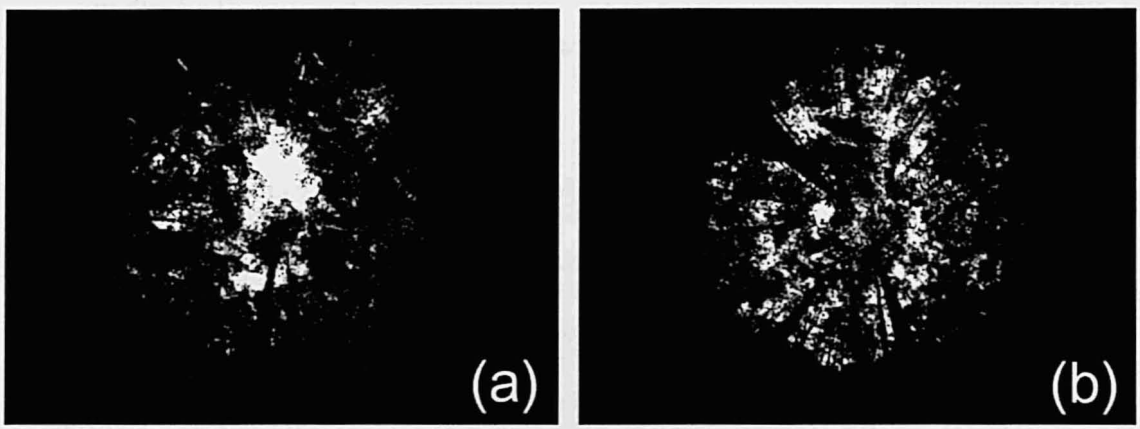

Figure 3-5. Hemispherical photographs of the (a) gap and (b) understory. The direct site factor was greater in gaps than in the understory because of the large opening, while the indirect site factor was greater in the understory because in gaps, the canopy around the opening was dense.

A number of factors affected morphology and allocation of seedlings. *F* values in the multiple regression models allow one to compare relative importance in morphology and allocation of biotic environments, abiotic environments and biomass. Of the dependent variables affected by biomass, biomass had the highest *F* values (Tables 2-3 and 2-4). This indicates that ontogeny has strong effects on morphology and allocation in natural seedling populations of the species studied.

The remaining seedlings may be filtered by specific environmental conditions, and the environmental factors that affected seedling morphology and allocation are limited because of the filtering effect. Since it is difficult to study morphology and allocation in natural populations (see Poorter 2001), here the effects of ontogenetic differences between two species were focused on.

While *S. glauca* did not show any changes in allocation patterns, *Stemonurus scorpioides* showed a drastic change. As biomass increased, root mass ratio decreased, stem mass ratio decreased and leaf mass ratio increased. It indicates that *S. scorpioides* constructs firm roots and stems first and then allocation to the growth of leaves increase.

Seedlings of *S. scorpioides* are often submerged when the water table is high. Their thick porometric roots considered to be needed for enduring flooding stress. Seedlings of *S. scorpioides* seldom increase leaf numbers during the study period (Table 3-2). The maximum leaf number was four (9 of 264 harvested seedlings). Most leaves that remained were cotyledons while the hypogeal cotyledons of *Swintonia glauca* were shed within the first three months. Instead of producing new leaves, they allocate resources to roots at a very young age.

In addition to a smaller production of new leaves by *Stemonurus scorpioides*, its biomass was lower than that of seedlings of *Swintonia glauca*, (Table 2-2) although *Stemonurus scorpioides* has larger seeds (see Species Studied). Therefore, the relative growth rate of *S.*

scorpioides seedlings is lower.

Seedlings with a lower relative growth rate, like *S. scorpioides*, characteristically tolerate low-light environments (Kitajima 1994; Poorter 1999) and water logging (McKee 1995). Turner (2001) concluded that flood-tolerance may have a physiological cost. The case of *S. scorpioides* is applicable to this conclusion, and it is regarded as stress-tolerant species.

3.5. Conclusion

In conclusion, survival and growth of seedlings of both species are affected by both light environment and elevational gradients. Survival and growth responses of seedlings of *S. glauca* to flooding and light environment were stress-intolerant, while the responses of seedlings of *S. scorpioides* showed higher stress-tolerance than seedlings of *S. glauca*. Also, morphological features of the study species supported the stress-tolerances of both species. Seedlings of *S. glauca* showed negative distant dependent mortality to conspecific parental trees in the understory, despite the mounded sites around conspecific adults. Thus, elevated sites except mounds around conspecific parental trees is important for regeneration for *S. seedlings*.

Plate 2. Patchy inundated forest floor.

Plate 3. Patchy inundated forest floor and a large tree of *Shorea* sp.

CHAPTER 4

Spatial assocations of tree species

4.1. Introduction

Spatial distribution of plants is likely to induce environmental heterogeneity by modification of the organic matter cycle (mainly through litter input to ground surface in the canopy and rooting zones) (Modelet et al. 1993, Belsky and Canham 1994, Rhoades and Sanford 1994, Pugnaire and Haase 1996, Schlesinger et al. 1996). Such effects of plant species on nutrient cycling can affect plant distribution at the individual level. One species that affect the nutrient cycling around them alter the soil properties. Such altered soil conditions affect plant species that can inhabit the immediate area. Thus, close relationships and spatial associations among modifying individual and inhabiting individual species can be assumed. If the species of the former and the latter are different, the process that affects the soil properties contributes to species coexistence.

Analyses of spatial point patterns of individual plants have been used for studying interactions among plant species and for investigating the structure of ecological communities. Results of spatial analyses enable us to infer the underlying processes: competition and mortality (Kenkel 1988, Duncan 1991), dispersal and competition (Sterner et al. 1986, Wei and Skarpe 1995, Nanami et al. 1999), disturbance and competition (Skarpe 1991), and testing or illustration of those methods (Fisher 1993, Moeur 1993). Recently, Tirado and Pugnaire (2003) used spatial point pattern analysis to link spatial patterns and environmental modification by canopy shading.

Studies that concurrently examine these interacting factors that occur among plant species through soil processes are intended to promote a better understanding of plant species

coexistence and ecosystem processes. In fact, many studies have suggested the possibility that spatial aggregation of plants is evidence of a positive interaction among clumped species (Haase et al. 1997, Kikvidze and Nakhutsrishvili 1998, Eccels et al. 1999, Condit et al. 2000, Miyamoto et. 2003). However, most studies that concurrently examine plant interaction through soil processes and spatial distribution in natural communities are rare. Very few studies have demonstrated linkage between habitat modifications generated by plant activity and plant species distribution. Callaway (1994) reported that the spatial correlation between shrub species and annual plants reflects modifications of the soil and light environment in salt marsh. Tirado and Pugnaire (2003) used spatial point pattern analysis to link spatial patterns and environmental modification by canopy shading and soil modification.

In the present chapter, I conducted spatial point pattern analysis among tree species in a tropical peat swamp forest. For the spatial point pattern analyses, as representative trees that are associated with specific microtopographic features, I defined established buttressed trees and non-mound-forming trees, respectively. In the present study, the definition of an established buttressed tree is a buttressed tree with dbh $\geq$ 40 cm that spreads large mounded sites around itself. This group includes individuals of *Swintonia glauca* Engl.(Anacardiaceae), *Shorea teysmanniana* Dyer, ex Brandis. (Dipterocarpaceae), *Shorea uliginosa* Foxworthy. (Dipterocarpaceae), *Aglaia argentea* Blume (Meliaceae), and *Palaquim burckii* H. J. Lam (Sapotaceae). The definition of an established non-mound-forming tree was a tree with dbh $\geq$ 15 cm around which relatively low elevated sites (non-mounds) are found (see below). This group includes individuals of *Ganua mottleyana* Pierre ex Dubard (Sapotaceae) and *Stemonurus secundiflorus* Blume (Icacinaceae). Using these trees as indices of two types of microtopography, I conducted spatial point pattern analyses.

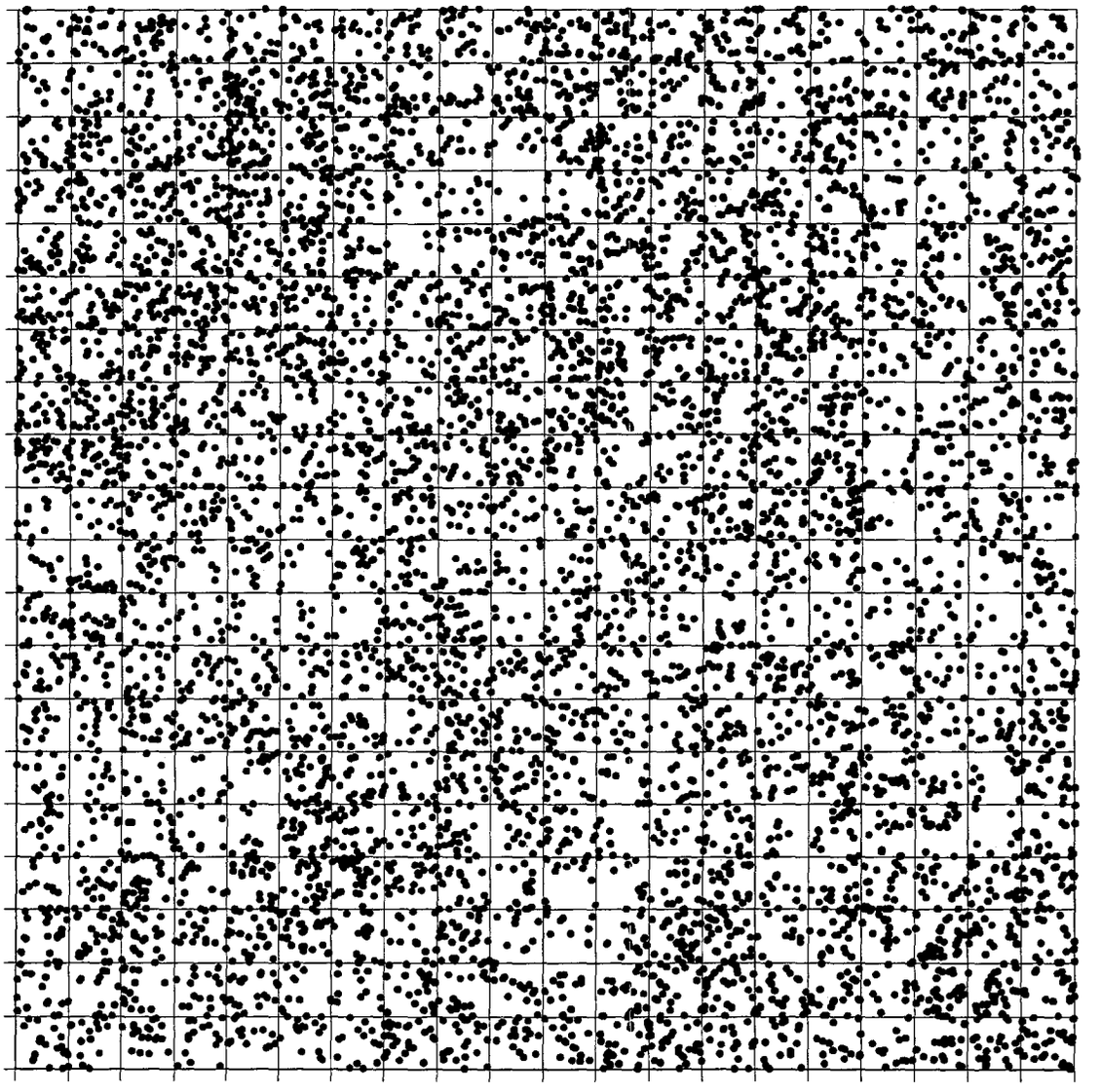

Figure 4.1. The spatial distribution of trees (dbh 1 cm) in the 100 m 100 m plot at Kermutan Wildlife Sanctuary, Riaru, East Sumatra, Indonesia.

Table 4-1. The top ten species over 1 cm in DBH by number. Abbreviations for life forms are C: canopy tree and E: emergent tree; and for morphology, B: buttressed root, CK: curved knee-root, SP: stick-like pneumatophore, and S: stilt root.

Species	Individual number	Max dbh	Root type	Canopy
Ganua mottleyana	1212	444	CK	C
Stemonurus secundiflorus	566	229	SP	C
Eugenia rhizophora	532	222	S	C
Calophyllum rigidum	484	250		C
Ilex pleiobrachiata	462	164		C
Knema intermedia	280	406	S	C
Tetractomia tetrandra	279	511		C
Swintonia glauca	244	688	B	E
Eugenia lepidocarpa	238	120	S	C
Ilex cymosa	231	321		C

4.2. Materials and methods

Plot design and Plant distribution

I laid out 1 ha study plots 1 km inland from the Kermutan River. Bores indicated that the peat depth was ca. 4-5 m in the study plots. The plot is an extension of a 0.6 ha plot in Momose and Shimamura (2002) (c.f. plot B). The type of forest is similar to a mixed swamp forest (Anderson 1961, Page et al. 1999). In the study plot, over 110 tree species exceeding 1 cm in dbh are found.

The study plot was a 1-ha square with edges running north-south and east-west. The mapping of trees was undertaken in 2000 for 0.6 ha of the plot. From August 2002 to March 2003, the plot was extended to 1 ha and re-census of all individuals was undertaken with reference to the former data for the first 0.6 ha. Thus, the data for 1 ha plots in the present study corresponds to the status of the plot at the latter term of the census. The 1 ha plot was carefully delineated and subsequently gridded into 400 contiguous quadrats of 5 × 5 m, using a pocket compass. Within each quadrat, the x and y coordination, the species, and the dbhs of all living trees (dbh ≥ 1 cm) were recorded. In Herbarium Bogoriense, Bogor, Indonesia, identification of specimens was conducted. Vouchers are deposited in the herbarium.

The census revealed 7941 individuals (Figure 4-1) more than 1 cm in dbh, and over 110 tree species within the plot. Among the top ten species in individual number, *Ganua mottleyana* have curved knee roots, *Stemonurus secundiflorus* have stick-like pneumatophoreses, and *Eugenia rhizophora* Boerlage et Koorders (Myrtaceae), *Knema intermedia* (Bl.) Warb. and *Eugenia lepidocarpa* Wall. (Myrtaceae) have stilt root. As previously reported in chapter 3, *Swintonia glauca* develops buttressed roots. *Calophyllum rigidum* Miq. (Cluseaceae), *Ilex pleiobrachiata* Loes. (Aquifoliaceae), *Tetractomia tetrandra* (Roxb.) Merrill (Rutaceae), and *Ilex cymosa* Blume (Aquifoliaceae) trees have no outstanding root structure (Table 4-1).

Microhabitats around huge trees

To study the microtopography around some groups of established trees, I selected living and dead established buttressed trees (dbh ≥ 40 cm) and seven individuals of established *Ganua mottleyana* and *Stemonurus secundiflorus* (dbh ≥ 15 cm). These trees were selected by computation from the tagged trees in the former 0.6 ha part of the study plot. To compare the mounds around buttressed trees between dead and living individuals, I did not distinguish the species of living buttressed individuals, because to identify species of dead established buttressed trees was impossible and because no remarkable difference was found in the size of mounds around living buttressed trees among species. For each individual, we laid out four 6 m transect lines running to each point of the compass from the center of the trunk. At 12 points placed every 50cm along the transects, I measured the elevation using the procedure mentioned in Chapter 3.

To estimate the light environment around established buttressed and non-mound-forming trees, I took hemispherical canopy photographs at a height of 1.0 m above the ground with a fish-eye camera (Cool Pix 900 with Fish-eye converter FC-E8, Nikon, Tokyo Japan) in March 2001. I selected five established buttressed trees and five individuals of *Ganua mottleyana* and *Stemonurus secundiflorus* (15 cm ≥ d.b.h.). These trees were selected randomly, by computation, from among the tagged trees in the former 0.6 ha plot of the study plot. For each individual, I laid out two transect lines running north and west from the center of the trunk to 5 m ahead. At 5 points placed every 1 m along the transects, I took hemispherical photographs. The images were processed using a software program (Hemiview, Delta-T device Ltd. Cambridge UK) to calculate the indirect site factor (ISF). As already mentioned in chapter 3, indirect estimation from hemispherical photography gives a reliable ranking of PPFD and its relative difference among sites (Engelbrecht and Herz 2001). I used ISF as an index of the light condition around established trees. To compare ISF around three tree groups we used the Kruskal-Wallis test.

Spatial point pattern analyses

I tested the spatial association of abundant species in the plot. The top ten species in individual number (Table 4-1) were considered as being abundant, and their spatial association to two groups of the established trees was tested. Established buttressed trees and established non-mound-forming trees were used as indices of the microtopography with which they are associated (see Figure 4-1).

The *K* function (Ripley 1977) considers the location of all individuals to describe the spatial pattern of a population, and the *L* function is obtained as $L(t) = \sqrt{K(t)/\pi} - t$ (Besag 1977) At a distance *t*, $K(t) = \pi t^2$ ($L(t) = 0$) indicates a spatially random population. A regular distribution is indicated by values less than πt^2, and a clumped distribution is indicated by values greater than πt^2.

The function $K_{1,2}(t)$ is a generalization of the function K(t), which is used to investigate the interrelationships between two patterns simultaneously. The resulting bivariate function $L_{1,2}(t)$ indicates whether two groups are spatially independent: $L_{1,2}(t)>0$ indicates attraction and $L_{1,2}(t)<0$ indicates repulsion (Upton and Fingleton 1985).

The statistical significance of the $L_{1,2}(t)$ vs. *t* diagram can be determined using Monte Carlo methods (Besag 1977, Besag and Diggle 1977, Marriott 1979)). The Monte Carlo approach is appropriate when testing for departures from spatial randomness (Kenkel 1988). This study used the values at the limit of the 2.5 % tails of 1,000 randomizations (mean±1.96 SD) for 95% confidence intervals by randomly re-positioning points in the plot. If the deviation of the sample statistic from zero expectation is significantly positive, the sampled points are assumed to be aggregated, while significant negative deviation suggests a regular (uniform) pattern (Diggle 1983). If the sample statistic remains within the bounds of the confidence interval at any given *t*,

the null hypothesis of complete spatial randomness cannot be rejected. Statistical analysis of the data was performed using the SPPA program (Haase 2001).

To detect the spatial association of tree species, I used the $L_{1,2}(t)$ function. Spatial associations of the top ten species in terms of individual numbers (Table 4-1) to established buttressed trees and established non-mound-forming trees were tested. Each tree species was divided into two groups: large and small trees. Large trees were the top 30% of individuals in terms of dbh of each species and small trees were the bottom 40% of individuals in terms of dbh of each species. Large trees of *Ganua mottleyana* and *Stemonurus secundiflorus* are the components of the established non-mound-forming trees and *Swintonia glauca* those of the established buttressed trees. Tests on spatial association of large *Ganua mottleyana* and *Stemonurus secundiflorus* trees to the established non-mound-forming trees were conducted by omitting trees 15 cm ≥ d.b.h. from large trees but not from established trees. Also, spatial associations of large *Swintonia glauca* trees to established buttressed trees were tested by omitting individuals 40 cm ≥ d.b.h. from large trees.

4.3. Results

Microhabitat around established trees

According to the measurement of elevation at transect lines around seven trees, mounds were found around the living and dead established buttressed trees. Mean elevation was 43.6 cm at points at a 0.5 m distance from the center of trunks of large living buttressed trees, and decreased gradually as the distance from tree trunks increased (Figure 4-2c,d). Around the established non-mound-forming trees, lower elevations than those around the living established buttressed trees were found; mean elevations were 11.3 cm and 7.2 cm at 0.5 m, respectively, and no explicit trend of decline or increment was recognized as the distance from tree trunks

increased (Figure 4-2a,b).

When the distance from tree trunks (all trees) was 3.5 m or more, mean elevations became mostly constant (6.75–12.2 cm) around the established living and dead buttressed trees. Thus, on average, the height of mounds around the living large buttressed trees was 34.1 cm (subtracting mean elevation at 3.5-6 m from that at 0.5m), and the radius was between 3.5 m and 4.0 m. On the other hand, the explicit radius of ground level sites around the established non-mound-forming trees was not found within 7 m. Within 3.5 m, the result of a test of homoscedasticity (Levene's test) and ANOVA showed significant differences in variances (F = 49.5, $p < 0.001$) and means among the types of established trees (F = 80.2, $p < 0.001$), respectively. In the results of multiple comparisons of means (Tamhane's T2 test), all pairs among four groups showed a significant difference ($p < 0.001$) except in the case of a pair of established non-mound-forming trees (n.s.).

Light environment around established trees

With regard to the light environment around the established trees within 5 m, no explicit changes in ISF according to distance from tree trunks was found (Figure 4-3) among tree types. Values of ISF did not show significant regression to distance from the center of the trunk of the established buttressed trees (F = 0.526, n.s.), the established G*anua mottleyana* trees (F = 1.72 n.s.), and the established *Stemonurus secundiflorus* trees (F = 0.301 n.s.). Mean ISF (SE) values around the established buttressed trees, the *Ganua mottleyana* trees, and the *Stemonurus secundiflorus* trees were 0.096 (0.0019), 0.099 (0.0015), and 0.10 (0.0020), respectively. The result of the Kruskal- Wallis test showed no significant difference among the three groups (χ^2 = 4.55, n.s.).

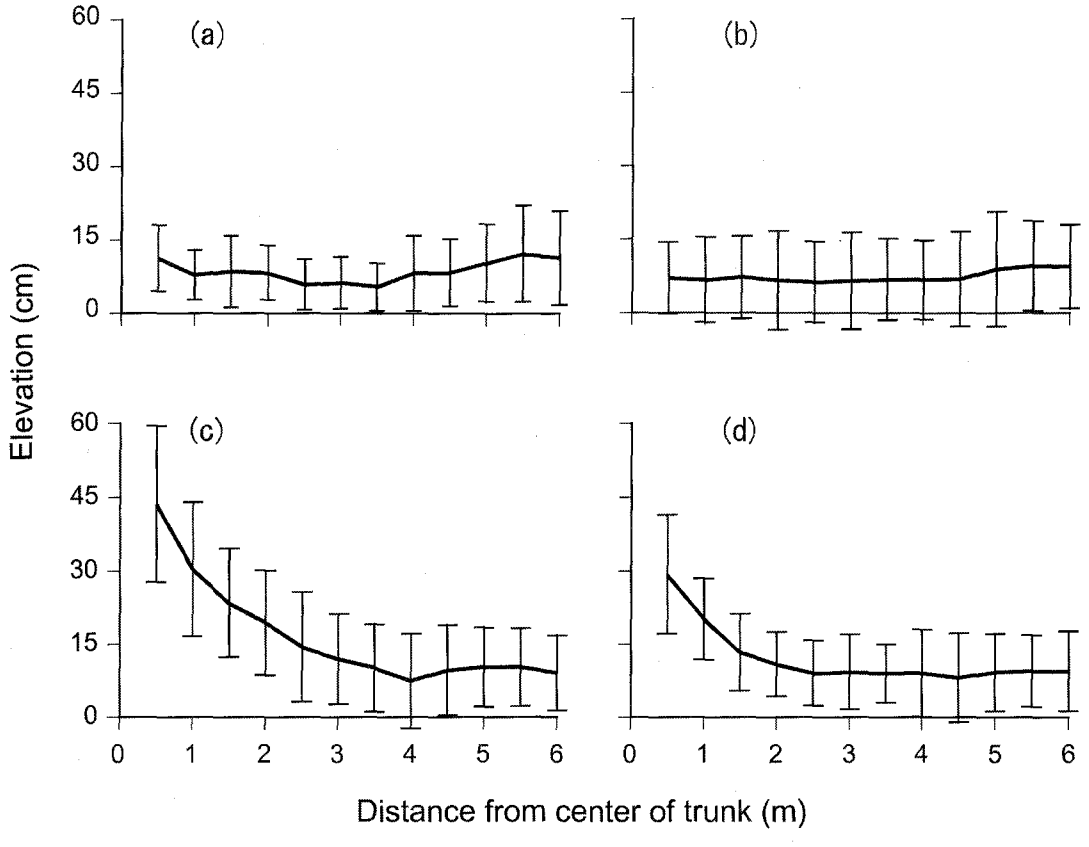

Figure 4-2. Changes in ground surface elevation with distance from established *Ganua mottleyana* trees (15 cm ≥ dbh) (a), *Stemonurus secundiflorus* trees (15 cm ≥ dbh) (b), living established buttressed trees (40 cm ≥ dbh) (c), and dead established buttressed trees (40 cm ≥ dbh) (d). Whiskers indicate estimated standard deviation for each group or species of tree.

Spatial associations of established buttressed trees

To clarify the role of mounds around the established buttressed trees, I paid particular attention to the spatial association between the established buttressed trees and tree species within 3.5 m of the distance that corresponded to the radius of mounded sites. Within that radius, both large and small trees of *Ganua mottleyana*, *Ilex pleiobrachiata, Eugenia lepidocarpa*, and *Tetractomia tetrandra* were spatially independent of the established buttressed trees (Table 4-2 and 4-3). Small *Calophyllum rigidum* and *Ilex cymosa* trees were spatially independent of the established buttressed trees, showing shifts in their patterns of distribution as they grow. Small trees of *Eugenia rhizophora* and *Swintonia glauca* showed no spatial association to the established buttressed trees. Distributions of these two species showed repulsion to the established buttressed trees as they grow. Small *Knema intermedia* trees were spatially attracted to the established buttressed trees. The distribution of the conspecific large trees indicated repulsion to the established buttressed trees (Table 4-2 and 4-3).

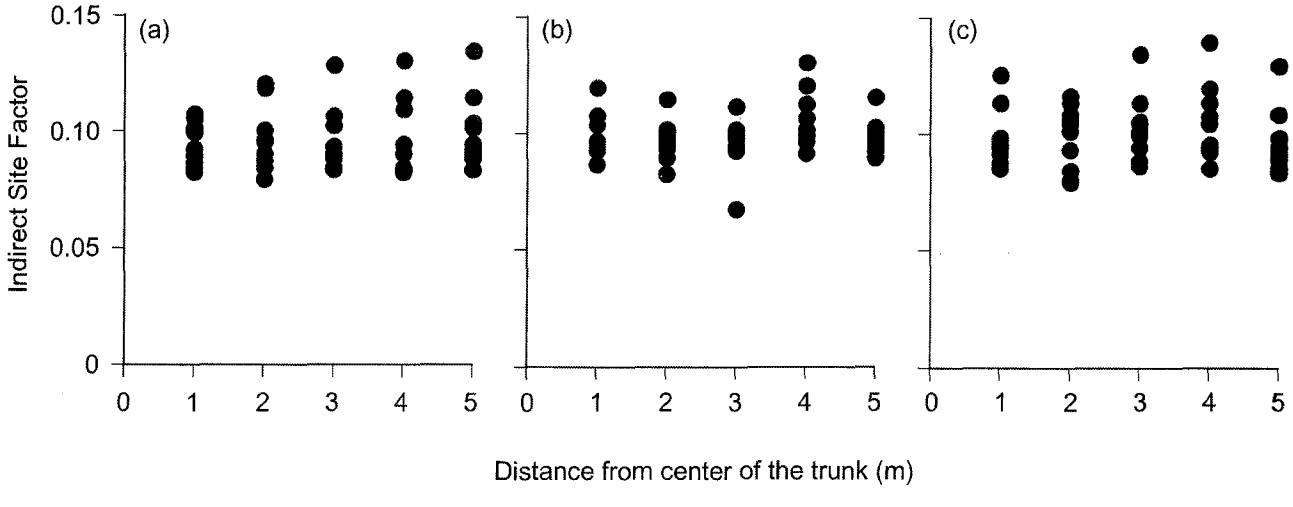

Figure 4-3. Changes in Indirect Site Factor with distance from established buttressed trees (40 cm ≥ dbh) (a), established *Ganua mottleyana* trees (15 cm ≥ dbh) (b), and established *Stemonurus secundiflorus* trees (15 cm ≥ dbh) (c).

Table 4-2. Significance of $L_{1,2}(t)$ values of bivariate distribution of established buttressed trees (dbh ≥ 40 cm) vs. small trees of each species. A dot indicates that the trees are spatially independent of established buttressed trees at a distance t (m). R and A indicate that the trees showed significant ($p < 0.05$) repulsion and attraction distribution to established buttressed trees at a distance t(m). The vertical broken line indicates the radius of mounds around established buttressed trees (3.5 m).

	Distance t (m)																			
Species	1		2		3			4		5		6		7		8		9		10
Ganua mottleyana	•	•	•	•	•	•	•	•	•	R	R	•	•	•	•	•	•	•	•	•
Stemonurus secundiflorus	•	•	•	•	•	•	R	•	•	R	R	R	R	R	R	R	R	R	R	R
Eugenia rhizophora	•	•	•	•	•	•	•	•	•	R	•	•	•	•	•	•	•	•	R	R
Calophyllum rigidum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ilex pleiobrachiata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Knema intermedia	•	•	•	A	A	•	•	•	•	A	A	•	•	•	•	•	•	•	•	•
Tetractomia tetrandra	•	•	•	•	•	•	•	•	•	•	•	•	•	R	R	R	R	R	R	•
Swintonia glauca	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eugenia lepidocarpa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ilex cymosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

Table 4-3. Significance of $L_{1,2}(t)$ values of bivariate distribution of established buttressed trees (dbh ≥ 40 cm) vs. large trees of each species. A dot indicates that the trees are spatially independent of established buttressed trees at a distance t (m). R and A indicate that the trees showed significant ($p < 0.05$) repulsion and attraction distribution to established buttressed trees at a distance t (m). The vertical broken line indicates the radius of mounds around established buttressed trees (3.5 m).

	Distance t (m)																			
Species	1			2		3		4		5		6		7		8		9		10
Ganua mottleyana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Stemonurus secundiflorus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eugenia rhizophora	•	•	R	•	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
Calophyllum rigidum	•	•	•	A	•	•	A	A	•	A	A	A	A	A	A	A	A	A	A	A
Ilex pleiobrachiata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	R	•	•	•	•
Knema intermedia	•	•	•	R	•	R	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Tetractomia tetrandra	•	•	•	•	•	•	•	•	•	A	•	•	•	•	•	•	•	•	A	A
Swintonia glauca	•	•	•	•	R	R	R	R	R	•	R	R	R	R	R	R	R	•	R	•
Syzigium lepidocarupum	•	•	•	•	•	•	•	•	•	•	•	R	•	•	•	•	•	•	•	•
Ilex cymosa	•	•	•	•	•	A	•	•	•	•	A	•	•	•	•	•	•	•	•	•

Spatial association of established non-mound-forming trees

As has already been indicated, around the established *Ganua mottleyana* and *Stemonurus secundiflorus* trees (= the established non-mound-forming trees) the ground-level site spread, and the radius of the ground-level site was at least ca 6 m. Here, I report on spatial association around established non-mound-forming trees within a 6 m distance.

For three of the ten species, small individuals showed significant spatial association to established non-mound-forming species. Small trees of *Ganua mottleyana* and were attracted to the established non-mound-forming trees (Table 4-4). The attracted distribution became independent at the large stage of *Ganua mottleyana* (Table 4-5). Small trees of *Calophyllum rigidum* also showed attracted distribution to the established non-mound-forming trees at a distance of 0.5 m, while distribution of conspecific large trees were repulsed from the established non-mound-forming trees (Table 4-4 and 4-5). Small trees of *Swintonia glauca*, and large conspecific trees, showed repulsed distribution from the established non-mound-forming trees. Small trees of the remaining seven species were spatially independent of the established non-mound-forming trees. Large trees of *Stemonurus secundiflorus*, *Knema intermedia*, *Tetractomia tetrandra*, and *Eugenia lepidocarpa* were spatially attracted to the non-mound-forming trees. The spatial association to established buttressed trees of the large trees of *Eugenia rhizophora* changes to repulsed distribution as they grow. Large trees of *Calophyllum rigidum* showed repulsed distribution to established non-mound-forming trees (Table 4-4 and 4-5).

Table 4-4. Significance of $L_{1,2}(t)$ values of bivariate distribution of the established non-mound-forming trees (dbh ≥ 40 cm) vs. small trees of each species. A dot indicates that the trees are spatially independent of established buttressed trees at a distance t (m). R and A indicate that the trees showed significant ($p < 0.05$) repulsion and attraction distribution to established buttressed trees at a distance t (m). The vertical broken line indicates the radius of non-mounded sites around non-mound-forming trees (6 m).

	Distance t (m)																			
Species	1		2		3		4		5		6		7		8		9		10	
Ganua mottleyana	•	•	•	•	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Stemonurus secundiflorus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eugenia rhizophora	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Calophyllum rigidum	A	•	•	•	•	•	•	•	•	•	•	•	•	A	A	A	•	•	•	•
Ilex pleiobrachiata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Knema intermedia	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	R	•	•	•
Tetractomia tetrandra	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Swintonia glauca	•	•	•	•	•	•	R	•	•	•	R	•	•	•	•	•	•	•	•	•
Eugenia lepidocarpa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ilex cymosa	•	•	•	•	•	•	•	•	•	•	•	•	A	A	A	A	A	A	A	A

Table 4-5. Significance of $L_{12}(t)$ values of bivariate distribution of established non-mound-forming trees (dbh ≥ 40 cm) vs. large trees of each species. A dot indicates that the trees are spatially independent of established buttressed trees at a distance t(m). R and A indicate that the trees showed significant ($p < 0.05$) repulsion and attraction distribution to established buttressed trees at a distance t(m). The vertical broken line indicates the radius of non-mounded sites around non-mound-forming trees (6 m).

	Distance t (m)																			
Species	1		2		3		4		5		6		7		8		9		10	
Ganua mottleyana	•	•	•	•	•	•	•	•	•	•	•	•	•	•	A	A	A	A	A	A
Stemonurus secundiflorus	•	•	•	•	A	•	•	A	•	A	A	A	•	•	•	•	•	•	•	•
Eugenia rhizophora	•	•	•	•	•	•	R	R	R	•	R	R	R	R	R	R	R	R	R	R
Calophyllum rigidum	•	R	•	•	•	•	•	R	•	•	•	•	•	•	•	•	•	•	•	•
Ilex pleiobrachiata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Knema intermedia	•	•	A	A	A	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Tetractomia tetrandra	•	•	•	•	•	•	•	•	•	•	•	A	A	A	A	A	A	A	A	A
Swintonia glauca	•	•	•	•	•	•	R	R	R	R	R	R	R	R	R	R	R	R	R	R
Eugenia lepidocarpa	•	•	•	A	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Ilex cymosa	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•

Table 4-6. Summary of spatial point pattern analyses for each pairs. R and A indicate that the trees showed significant ($p < 0.05$) repulsive and attractive distribution to established buttressed trees within a certain radius. For established buttressed trees the radius is 3.5 m, and for non-mound-forming trees the radius is 6 m. Abbreviations for flooding-tolerance are +: flooding-tolerant species, -: flooding-intolerant species.

	Established buttressed trees		Non-mound forming trees		Flooding-tolerance
Species	Small trees	Large trees	Small trees	Large trees	
Ganua mottleyana			A		
Stemonurus secundiflorus	R			A	+
Eugenia rhizophora		R		R	
Calophyllum rigidum		A	A	R	-
Ilex pleiobrachiata					
Knema intermedia	A	R		A	+
Tetractomia tetrandra				A	+
Swintonia glauca		R	R	R	
Eugenia lepidocarpa				A	+
Ilex cymosa		A			-

4.4. Discussion

Spatial associations of tree species

This study demonstrated that mounds were spread around the established buttressed trees, and ground level sites were spread around the established non-mound-forming trees. In wetlands, microtopography is known to contribute to plant species distribution. Given that relative distance between the water table and the soil surface determine the degree of inundation, the distribution of plant species is arranged along the elevation according to species flood tolerance (Robertson 1978, Jeglum and He 1995). The light environment is also known to affect plant species distribution. Given that there were no differences in ISF between the two established tree groups (Figure 4-2), the difference in distribution of tree species between the sites around the two established tree groups was mainly attributed to effects of microtopography.

Because relative elevation between the water table and the soil surface often results in plant species being arranged according to their flood-tolerance, along the gradient of water tolerance there are stress-tolerant and stress-intolerant species. Stress-tolerant species often require stressful habitats, where competitive species are excluded. On the other hand, stress-intolerant species require a comparatively less stressful habitat. On the study site, mounds spread around the established buttressed trees represent a less stressful habitat; the relatively high elevation is protective against inundation. Ground level sites that spread around the established non-mound-forming trees represent a stressful habitat, because the relatively low elevation increases the intensity of inundation. Thus, the tree species attracted to the established buttressed trees or repulsed from the established non-mound-forming trees are flood-intolerant individuals, whereas the tree species attracted to established non-mound-forming trees or repulsed from established buttressed trees are flood-intolerant species.

It has been often documented that distribution, especially for juveniles and seedlings, is strongly affected by the plant's means of dispersal (Hubbell 1979, Briggs and Gibson 1992). Small dispersal distances (as discussed by Prentice and Werger 1985, Sterner et al. 1986, Hatton 1989) explain the clumped distribution of small trees, and wide range dispersal (bird dispersal) indicates a high proportion of seed transport from the vicinity of the parent plants (Holthuijzen et al 1987). Of course, the distribution of parent plants also affects the spatial heterogeneity of small plants. It is difficult to distinguish whether the observed pattern of distribution for small trees is due to dispersal or habitat preferences of each species. However, a comparison of the pattern of distribution between small and large conspecific trees completely eliminates the effect of means of seed dispersal. The difference in distribution reflects post-dispersal events. Thus, such a comparison is very informative to an analysis of their habitat preference. Here, I focus on shifts in distribution between small trees and large trees to explain the habitat preference of tree species.

As already indicated in the previous section, to clarify the role of mounds around the established buttressed trees, I paid particular attention to significant spatial associations between the established buttressed trees and tree species within 3.5 m, which distance corresponds to the radius of mounded sites. Also, to clarify the role of non-mounded sites around the non-mound-forming trees, I discuss significant spatial associations between the established non-mound-forming trees and tree species within a distance of 6 m (Figure 4-6.).

Attractive distribution to the established buttressed trees was found in *Calopyllum rigidum* and *Ilex cymosa* trees in large stages. Small trees of the two species were independent of the established buttressed trees. The shifts in distribution can be attributed to species flood-tolerance and associated effects of microtopography. In addition, the shift in distribution of *Calophyllum rigidum* trees toward repulsion from the established non-mound-forming trees

with increase in size class also supports that *C. rigidum* trees are flood-intolerant (Table 4-2 and 4-3).

An explanation of the shifts in distribution toward less aggregation as size class increases requires some caution. An overall tendency toward a less aggregated pattern along the life cycle has been found in tree species (Sterner et al. 1986, Kenkel 1988). This decreasing degree of aggregation can often be attributed to density-dependent mortality (Clark and Clark 1984). If such observed decrease in aggregation of *C. rigidum* trees is due to density dependent mortality, such density dependent mortality also occurs around the established buttressed trees. Thus, the resulting spatial association between large *C. rigidum* trees and the established buttressed trees should be still one of repulsion or random. However, the observed pattern between large *C. rigidum* trees and the established buttressed trees was one of attraction. Therefore, it is natural to consider that a mound is a preferable habitat for *C. rigidum* trees and that the species is flood-intolerant. A similar explanation is applicable for the case of *Ilex cymosa* trees, which are also flood-intolerant (Table 4-2 and 4-3).

Spatially repulsive distributions to the established buttressed trees of large trees of *Eugenia rhizophora*, *Knema intermedia*, and *Swintonia glauca* were found. Small trees of these repulsed species were spatially aggregated to or independent of the established buttressed trees. As already indicated, such decrease in attraction with growth increases makes it difficult to determine whether the observed pattern is due to species flood-tolerance or density dependent mortality. According to spatial association with the established non-mound-forming trees, large *Kenema intermedia* trees were aggregated to them, while conspecific small trees were repulsed from them (Table 4-4, 4-5). If density dependent mortality occurs, the distribution of large *K. intermedia* trees would show repulsion to the established non-mound-forming trees. However, large *K. intermedia* trees were spatially aggregated to non-mound indicating trees. Thus, the *K.*

intermedia trees are flood-tolerant. On the other hand, large *Eugenia rhizophora* trees changed distribution from attraction to repulsion to the established buttressed and non-mound indicating trees as size class increases. It is not reasonable to explain the distribution of *E. rhizophora* trees by their flood-tolerance. Density dependent mortality may be a more reasonable explanation for the spatial distribution of *E. rhizophora*.

The shift in distribution of *Swintonia glauca* trees was similar to that of *Eugenia rhizophora*. However, it should be noted that this species is a component of established buttressed trees. Thus, the result of this study cannot exclude the possibility that the repulsion distribution to established buttressed trees of large *Swintonia glauca* is caused by density dependent mortality. In addition, some large trees of *S. glauca* are larger than the established non-mound-forming trees (Table 4-1). It is apparent that some individuals of this species occupied their habitat before the growth of the established non-mound-forming trees (16 individuals of 72 large individuals were larger than 15 cm in dbh, which is the threshold of the established non-mound-forming trees). Thus, some individuals of *S. glauca* raise the ground surface around them, and affect the growth of the established non-mound indicating trees. The data presented here is insufficient to explain whether the observed pattern was due to the flood-tolerance of *S. glauca* trees. However, seedling mortality of *S. glauca* was relatively high at lower elevation (Chapter 3). The repulsion distribution of small *S. glauca* to the established non-mound-forming species may be due to the flood-intolerance of *S. glauca* seedlings.

Adult trees of *Eugenia lepidocarpa* and *Tetractomia tetrandra* were spatially aggregated to the established non-mound-forming trees, while small trees of the two species were independent of the established non-mound-forming trees. As already discussed, such shifts in distribution towards attraction as size class increases are unexplainable by density dependent mortality; these two species are flood-tolerant species (Table 4-4 and 4-5).

Ganua mottleyana and *Stemonurus secundiflorus* constitute the established non-mound-forming trees. Small trees of *Ganua mottleyana* are spatially attracted to the established non-mound-forming trees, while large trees of *G. mottleyana* were spatially independent of the established non-mound-forming trees. Such a shift in distribution towards repulsion to conspecific large trees has often been reported (Nanami et al. 1999), and density dependence and/or distance from conspecific adult dependent mortality (Clark and Clark 1984) have been used by way of explanation. The data presented here, as in the case of *Swintonia glauca* trees, is insufficient to explain whether the observed pattern was due to the flood-tolerance of *G. mottleyana* trees. However, density dependent mortality or distance dependent mortality cannot explain the shift in distribution towards aggregation to the established non-mound-forming trees as the size of these individuals increases. Thus, *Stemonurus secundiflorus* are flood-tolerant species.

4.5. Conclusion

Excepting *Ganua mottleyana*, *Stemonurus secundiflorus*, and *Swintonia glauca*, which are components of the established buttressed or non-mound-forming trees, the distribution of five of the remaining seven tree species indicate that their distribution is affected by microtopographic heterogeneity associated with their degree of flood-tolerance. The spatial point pattern analyses indicate that *Calophyllum rigidum* and *Ilex cymosa* are flooding-intolerant species, and *Knema intermedia*, *Eugenia lepidocarpa*, and *Tetractomia tetlandra* are flood-tolerant species. Thus, the results presented in this chapter support the hypothesis that the spatial distribution pattern was a consequence of a microtopographic interaction associated with the established buttressed and/or non-mound-forming trees, and that microtopographies contribute to species coexistence in this forest. Thus, spatial heterogeneity of the microtopographic form provides an axis of

habitat partitioning in the tropical peat swamp forest.

Plate 4. Pneumatophores and seedlings of *Stemonurus scorpioides*.

Plate 5. Curved knee root of *Ganua mottleyana*.

CHAPTER 5

Organic matter dynamics

5.1. Introduction

In tropical forests, the amount and rate of litterfall and decomposition show considerable spatial variation, due to variations in canopy architecture and tree species (Tilman 1982). This spatial heterogeneity allows the coexistence of species and contributes to niche differentiation for seedlings (Molofsky and Augspurger 1992). Spatial heterogeneity is expected to be particularly prominent in tropical rain forests because of the variable canopy structure and extremely high species diversity found in these forests (Richards 1996). Thus, some studies have focused on the effect of such spatial heterogeneity (Alvarez and Becerra 1996, Burghouts et al. 1998). Also, in forested wetlands, the rate of below-ground production shows considerable spatial variation, due to variations in root structure and tree species. This spatial heterogeneity also contributes to species coexistence (Huenneke and Sharitz 1986). Thus, both above- and below-ground heterogeneity in organic matter dynamics is important in forested wetlands. However, despite its importance to the mosaic-like growth cycle of rain forests (Whitmore 1990), this spatial heterogeneity of above- and below-ground organic matter dynamics has received little attention in investigations of tropical wetlands.

As already suggested in Chapter 1, tropical peat swamp forests are characterized by considerable heterogeneity of surface topography. In particular, mounds spread around buttressed trees are one of the prominent microtopographies. And mounds in tropical peat swamp forest contribute to species coexistence (see Chapter 3,4). In tropical peat swamp forests, because peat that supports the terrestrial ecosystem originated from plant materials, plant activities regulate the conditions of peat surface (mound or non-mound) on a small scale. The

surface peat materials are of modern age (post 1950 AD) in Sumatran peat swamp forests (Maloney and McComac 1995, Brady 1997). This suggests that peat surface conditions are vulnerable to organic matter input and decomposition. Thus, organic matter dynamics at the local level determines the conditions--i.e., mounds and non-mounds--of the peat surface. For example, where production exceeds decomposition, the peat surface may be rising and a mound will be created. Where the rate of decomposition exceeds production, the peat surface may be sinking. Mass of production is due mainly to activity of large individuals on a small-scale level. Thus, large individuals may determine the condition of the peat surface (mound or non-mound) at the local level. Here we can assume a spatial association between specific microtopography and large individuals of specific trees. For example, a huge buttressed tree spreads a mounded site around itself by highly aggregated above- and below-ground production, while an individual without buttresses does not spread mounds around its. As already indicated in chapter 4, mounds around dead buttressed trees are sinking. This suggests that the rate of decomposition exceeds the rate of production in such gaps. Such differences in microtopography may be due to differences in the respective regimes of production and decomposition.

Here, I hypothesize that different microtopographies show different regimes of organic matter dynamics. To examine the above hypothesis, I conducted research on above- and below-ground production and decomposition. This research mainly focused on mounded sites around established buttressed trees, ground level sites (non-mounds) under the forest canopy, and gaps. Specific hypotheses for production and decomposition were addressed: (1) productivity at microsites would be the greatest on mounds and the least in gaps; (2) the rate of decomposition would be the greatest on mounds because of their well-aerated conditions; (3) in gaps, the balance between the rate of production and decomposition actually indicates that the peat surface is sinking; and (4) in mounded sites, the balance between the rate of producton and

decomposition actually indicates that the surface of the mounded site is rising or instable.

5.2. Materials and methods

Litter trap method

Litter fall was collected from the beginning of September 2001 to August 2002 at monthly intervals. Each litter trap was 1 m in diameter, and consisted of 2 mm mesh nylon netting suspended from a wire hoop and held 1 m above the ground. Ten traps were placed 1 m south of the trunks of established buttressed trees selected randomly. Ten traps were placed along a transect line. The transect line consists of the 9th quadrats from the west boundary of the study plot and runs from north to south. At the center of each two quadrats, along the transect line, litter traps were erected. In case this was too close to large buttressed trees, I changed the locations of the litter traps to the nearest quadrats that were considered to be well separated from the buttressed tree. The rest of the ten litter traps were located at the ten gap plot.

During the collection of litter fall, litter traps broke or were stolen three times, making the total collection times for gaps and mounds 119 and 118, respectively. After each collection of litter fall, litter samples were immediately dried in a self-made drying room to constant weight. They were divided into leaf litter, woody material, reproductive organs, and other, and then weighed.

Ingrowth core method

Ingrowth cores (20 cm length, 7 cm diameter), which were made of 2 mm nylon mesh, were filled with root-free peat and installed in the peat surface. The peat used for this purpose was taken from a nearby location; care was taken to fill the cores to bulk densities similar to the original levels. From each category of sites where litter traps had been placed, four sites were randomly

selected and a pair of ingrowth cores was inserted. Four pairs of ingrowth cores were installed 2 m north of trunks of established buttressed trees (mounded site). Under each of four ground level sites under the forest canopy and at four gap sites, a pair of ingrowth cores were also installed. Thus, 24 ingrowth cores were inserted (eight replications and three treatments). A set of cores was buried in August 2001 and harvested one year later.

At harvest, each ingrowth core was severed from the surrounding soil and removed. At the removal four cores had been broken. Consequently, the sample numbers became eight, six, and six for mounds, non-mounds, and gaps, respectively. Fine roots were separated from peat. After transport to the laboratory, root samples of each core were dried at 80 °C until they reached constant mass and then weighed. The mass of the root was log transformed before analysis, because its distribution was closer to log normal than to normal.

Wood decomposition experiments

Decomposition processes of wood materials of *Palaquim burckii* H. J. Lam were studied by a wood bag method. I excised wood blocks from a large trunk of *P. burckii*. The trunk had been cut during commercial logging. The diameter of the part of the trunk from which the blocks were cut was ca. 50 cm. From the center of the section, I cut out a hylic bar of heartwood. I divided the hylic bar into 125 samples of 6 × 6 × 3 cm block. These wood blocks were stored in a self-made drying house until they reached constant mass. The weight of each sample was recorded. Five samples were stored as control samples. The rest of the blocks were enclosed in mesh bags with a mesh size of approximately 15 mm. A total of 80 bags were prepared. The decomposition study covered a 36-month period from December 1999 to November 2002. Because this experiment commenced before the establishment of the study plot (Chapter 4), I selected five mounds of buttressed trees. On each mound, three samples of bags were placed and tied to stakes. I selected

15 ground level sites near the study plot. At each site, I placed blocks at ground level and buried blocks at 10 cm, 20 cm, and 40 cm below-ground (five replicates). For this experiment, each set of four wood blocks was tied at appropriate intervals and connected to stakes inserted at each site. Upon removal in May 2000 (25 bags), November 2000 (25 bags), and November 2002 (25 bags), the blocks were taken and dried in a self-made drying house for 5 days.

After transport to the laboratory, the losses of dry weight were determined after drying the samples to a constant weight at 80 °C. To adjust for the difference in the quality of the drying process between oven-drying and field drying (in the self-made drying house), I used the mean ratio of the weight of field-dried to the weight of oven-dried control samples as a coefficient that adjusts for the initial sample mass. Subsequently, losses were expressed as a percentage of the estimated dry weight.

Leaf litter decomposition

Decomposition processes of leaf litter of *Swintonia glauca* were studied by a litter bag method (Crossley and Hoglund 1962). To collect leaves of *S. glauca*, 10 litter traps (1 m in diameter) were placed where large *S. glauca* trees are abundant near the study plots from January 2001 to August 2001. Every month, the leaf litter was collected and the leaves of *S. glauca* were separated out. The leaves were dried in the self-made drying house until they processed in the laboratory In August, the leaves were dried again to constant mass. The litter (10 g) was enclosed in a litter bag (20 cm × 10 cm) made of polypropylene cloth with a mesh size of approximately 2 mm. A total of 110 litterbags were prepared. Five initial samples were preserved for further analyses.

Litterbags were set in August 2000. Within the study plot, five mounds of established buttressed trees were randomly selected by computation. Five ground level sites along the

transect line for litter trapping that avoided mounded sites and five gaps around the study plots were also selected. Before placement of litterbags, I tagged all litterbags and preestablished the harvest time of each sample. I placed seven litterbags at each selected point. Sampling of the bags took place seven times. Samples were taken monthly for the first two months, then bimonthly until August 2001. On each sampling, the collected litter samples were dried and placed in envelopes until processing. Unfortunately, at harvest some samples had been lost or the bags ripped. I successfully collected samples from 30 bags from mounds and from 31 bags from ground-level sites and gaps.

After transport to the laboratory, the losses of dry weight were determined after drying the samples to a constant weight at 80 °C. To adjust for the difference in the quality of the drying process between oven-drying and field-drying (in the self-made drying house), I used the mean ratio of the field-dried weight to the oven-dried weight of initial samples as a coefficient to adjust the initial sample mass. Then, losses were expressed as a percentage of the estimated dry weight.

Peat sampling

In October 2002, peat samples for chemical analyses were collected from the peat surface around the litter traps. From living and dead established buttressed trees, ground level sites, and gap sites, I selected five sites randomly, and three samples of peat materials were collected at each of them (3 replicates × 5 sites × 4 treatments). Samples were collected at ca 1.5 m from the center of the trunk or the stumps of living and dead established buttressed trees, and 2.5 m from the center of the litter trap (for ground and gap sites) to the north, east, and west of the bole. When traces of disturbance from the previous study could be seen, samples were taken at the nearest intact site.

In addition, amount of 40 volumetric samples of intact peat were extracted from the surface

layer using open-ended coring tubes of pipe 1061 cm^3 (diameter 11.8 cm, length 9.7 cm) in August 2003. From each site, two samples of peat materials were collected. Samples were collected at ca 2 m from the center of the trunk or sump of the selected living/dead established buttressed trees, and 2.5 m from the center of the selected litter trap (for ground and gap sites) to the east and south of the bole (2 replicates × 5 sites × 4 treatments). The samples were dried in the self-made drying house to constant mass, and then weighed. Dry bulk density was calculated as dried mass divided by the field volume of each sample, and expressed in g cm^{-3}.

Chemical analyses

Chemical analyses on litter fall and peat materials were conducted. Samples of litter fall collected in September and November 2001, when they showed the highest mass of litter fall, were analyzed. Litter and peat samples were oven-dried at 80 °C to constant mass, and then ground in a mill to pass through a 0.5 mm mesh sieve. Total carbon and total nitrogen contents were measured by automatic gas chromatography (NC analyzer SUMIGRAPH NC-900; Sumitomo Chemical Co., Osaka, Japan). After an acid wet oxidation in HNO^3, flame photometry (Clinical Flame Photometer PHP7, Jenway Ltd., Dunmow, Essex, UK) was used for measurements of calcium and sodium, and Inductively Coupled Plasma Atomic Spectrometry (IRIS CID, Thermo Electron K. K., Kanagawa, Japan) was used for measurements of phosphorus, potassium, and magnesium.

Data analyses

Decomposition rates of the leaf litter and the wood block were estimated by Olson's k (Olson 1963) according to the following equation:

$$W_t = W_0 \times \exp(-kt),$$

where W_t is the litter or timber weight after a given period, W_0 is the original litter weight, k is the decomposition rate, and t is the time. To test for the difference in decomposition constants among treatments, I used Z test for every pair of treatments. We used 0.167 and 0.005 for leaf litter and wood block, respectively, as the p value for significance in order to avoid the type I error generated by replicating tests.

To compare masses of litter fall, fine root production, and chemical components of litter fall and peat matrix, I used analysis of variance (ANOVA) using the general linear model command in SPSS 10.0J for Windows. Test homogeneity of variance (Levene's test) was performed before carrying out each comparison. When the null hypothesis of homoscedasticity among treatments was rejected, we used Tamhane's T2 test (Hochberg and Tamhane 1987) for multiple comparison. If the null hypothesis was not rejected, I conducted a multiple comparison by Bonfferoni's method.

5.3. Results

Litter fall mass

Mass of litter fall around established buttressed trees, under the forest canopy, and in gaps was determined. There were consistent seasonal patterns of litter fall among the three types of sites. There was an increase in litter fall during November and December 2001, when the precipitation was relatively high. Litter production between January and June 2002 was constant in all three types of sites (Figure 5-1).

There was a significant effect of site on annual rates of litter fall for leaf, wood, and total materials. In terms of total litter fall, that of leaves, woods, and overall mean litter fall were highest on mounded sites around established buttresses, and lowest in gaps (Table 5-1).

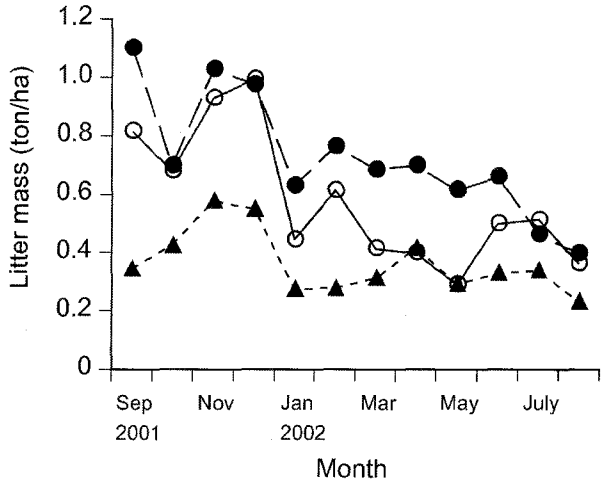

Figure 5-1. Monthly rates of litter fall for the three types of sites. ●: mounds around established buttressed trees. : ○ ground level site under forest canopy. ▲: gaps.

Table 5-1. Statistical results for each component of annual litter fall among the three types of sites ($df = 2$). Means (ton/ha/month) followed by a similar letter were not found to be significantly different ($p < 0.05$).

Variables	F	Mean (± 1 SE)		
		Gap	Mound	Non-mound
Total	53.9***	4.35[a]	8.67[b]	6.96[c]
		(0.235)	(0.432)	(0.347)
Leaves	43.2***	3.79[a]	6.72[b]	5.25[c]
		(0.221)	(0.323)	(0.227)
Wood	7.27***	0.301[a]	0.847[b]	0.815[c]
		(0.0420)	(0.175)	(0.116)

*$p < 0.05$; **$p < 0.01$,*** $p < 0.001$

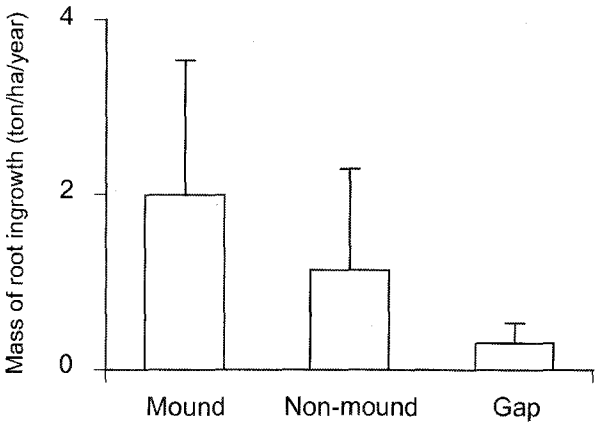

Figure 5-2. Mean values (SD) of estimated annual fine root production at each of the three types of sites.

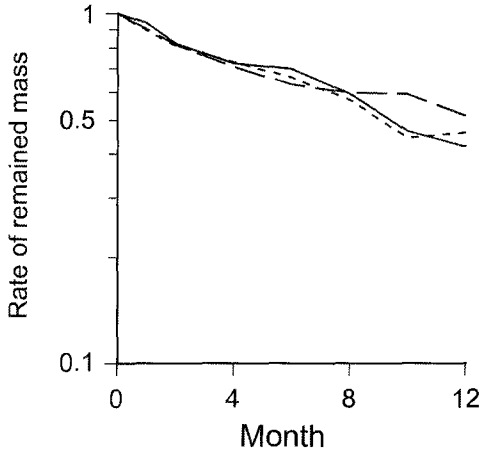

Figure 5-3. Changes in weight of post-drying *Swintonia glauca* leaf litter during the decomposition. Solid, dotted, and broken lines indicate the post-drying mass for mounds around established buttressed trees, ground level sites under forest canopy, and gaps.

Ingrowth core experiment

There was a significant effect of site on annual rates of fine root production ($F_{2,17} = 4.22$, $p < 0.05$, log transformed). The rank of fine root production among the three types of sites was mounds around established living buttressed trees > ground level sites > gaps. Mean rates of estimated fine root production (SE) were 1.99 (0.585), 1.14 (0.517) and 0.307 (0.0985) ton/ha/year for mounds, non-mounds, and gaps, respectively. In addition to that geometric mean rates of fine root production (± SE) were 1.47 (1.98, 0.628), 0.478 (0.988, 0.0806) and 0.234 (0.327, 0.102) ton/ha/year for mounds, non-mounds, and gaps, respectively. The results of multiple comparison indicated that a significant ($p < 0.05$) difference between mounds and gaps, though no significant difference was found between gaps and ground level sites or between mounded sites and gaps.

Leaf litter decomposition

The rank in leaf litter decomposition rates (k) among the three types of sites was ground level sites > mounds around established buttresses > gap sites. Estimated decomposition rates (SE) were 0.0763 (0.00502), 0.0742 (0.00341), and 0.634 (0.00328) /month for ground level sites, mounds, and gaps, respectively (Figure 5-3). According to Z tests, there were no significant differences among any pairs ($p > 0.0167$). Without the correction of p values for the multiple comparison procedure, decomposition constants in gaps differed from those in mounds and ground level sites ($Z = 2.30$, $p < 0.05$, $Z = 2.16$, $p < 0.05$, respectively), while there was no difference between ground level sites and mounds ($Z = 0.346$, n.s.).

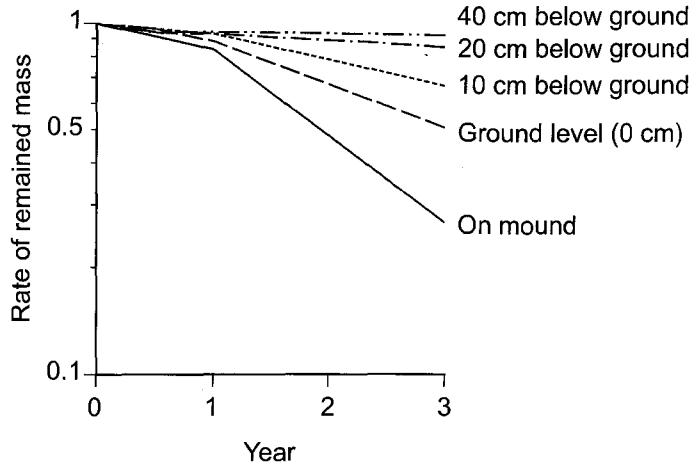

Figure 5-4. Changes in weight of post-drying *Palaquim bankanus* wood block during the decomposition.

Wood decomposition

The rank in terms of decomposition constant of wood blocks of *Palaquim burckii* of the five treatments was consistent with gradient of elevation, and the decomposition rate (k) was highest on mounds and lowest 40 cm below-ground. Estimated decomposition constants (SE) were 0.562 (0.104), 0.260, (0.0550), 0.135 (0.0211), 0.0570 (0.0112), and 0.030 (0.00581) /year for mounds, ground level, 10 cm below-ground, 20 cm below-ground, and 40 cm below-ground, respectively (Figure 5-4). Results of Z tests between all pairs of treatments, by using the correction of p values, indicate that all pairs of treatments showed a significant difference ($p <$ 0.005) in decomposition constants of wood blocks (Z values varied 3.18 - 4.91), except in the cases of three pairs, as follows: mounds and ground level (0 cm), ground level (0 cm) and 10 cm below-ground, and 20 cm and 40 cm below-ground (Z =2.47, 2.04, 2.00, respectively n.s.). Without the correction of p values, a significant difference ($p < 0.05$) was found between all pairs.

Peat properties

The bulk density of peat was significantly higher in non-mounded sites than mounded sites. Concentrations of total Na also differed between mounds and non-mounds (Table 5-2). In contrast to concentrations of Na, concentrations of N, C, K, and Mg differed between canopy gaps and under the forest canopy, but not between mounds and non-mounds. Ca concentrations were different according to both microtopographic types and canopy types. The significant effects of canopy × microtopography interactions were detected in concentration of Na, Ca, and P. This interaction was the only factor that showed a significant difference in P concentrations. Concentrations of Ca were highly fluctuant. The highest value of Ca concentration (10.8 mg/g) was found in mounded sites around the dead buttressed trees, while the lowest value of Ca concentration (2.47 mg/g) was found in mounded sites around the living established buttressed trees. There was no significant difference in C/N ratio in terms of microtopographic type or canopy type.

Leaf chemical component

The N concentrations in litter fall differed between mounds and ground level sites ($p < 0.05$) (Table 5-3). Concentrations of C, K, Na, Ca, Mg, and P in litter fall showed no significant differences among sites. Similar to N concentrations, the C/N ratio of litter fall differed between mounds and ground level sites ($p < 0.05$). Of the chemical components studied, only N concentrations differed among the three types of sites.

Table 5-2. Concentration of resource quality attributes in peat samples among four sites.

Canopy type	Open		Closed		*F* value		
Microtopography type	Non-mound	Mound	Non-Mound	Mound	Canopy	Micropography	A × B
N mg/g	24.4	23.3	25.5	25.4	5.9*	0.81	0.60
	(0.618)	(0.894)	(0.574)	(0.311)			
C mg/g	532	535	547	547	9.1**	0.089	0.12
	(5.78)	(5.15)	(4.10)	(1.54)			
K mg/g	0.440	0.406	0.558	0.706	26***	1.1	3.4
	(0.0345)	(0.0431)	(0.0405)	(0.0543)			
Na mg/g	0.119	0.103	0.177	0.0864	1.1	10**	4.4*
	(0.0146)	(0.0150)	(0.0121)	(0.0195)			
Ca mg/g	4.31	10.8	3.65	2.47	15***	5.0*	12***
	(0.625)	(2.06)	(0.502)	(0.360)			
Mg mg/g	1.11	0.975	1.37	1.72	14***	0.69	3.3
	(0.0926)	(0.153)	(0.114)	(0.176)			
P mg/g	0.544	0.410	0.437	0.487	0.077	1.3	4.6*
	(0.0341)	(0.0423)	(0.0436)	(0.0450)			
C/N	22.0	23.6	21.7	21.6	2.15	0.90	1.1
	(0.635)	(1.29)	(0.600)	(2.98)			
Bulk density	0.119	0.116	0.121	0.104	1.2	4.1*	1.9
	(0.00431)	(0.00429)	(0.00620)	(0.00383)			

*$p < 0.05$; **$p < 0.01$,*** $p < 0.001$

Table 5-3. Concentration of resource quality attributes of samples from litter trap at three sites. Means followed by a similar letter were not found to be significantly different ($p < 0.05$).

Canopy	Open	Closed	Emergent	
Microtopography	Gap	Flat	Mound	*F* value
N mg/g	12.9[ab]	13.3[a]	12.0[b]	3.64*
	(0.399)	(0.283)	(0.390)	
C mg/g	525	526	534	2.01
	(3.17)	(3.75)	(3.12)	
K mg/g	3.40	3.54	2.89	1.23
	(0.418)	(0.261)	(0.167)	
Na mg/g	0.101	0.111	0.123	2.24
	(0.00568)	(0.00842)	(0.00801)	
Ca mg/g	11.4	12.0	12.2	0.277
	(0.603)	(1.13)	(0.669)	
Mg mg/g	4.37	4.25	4.35	0.0454
	(0.299)	(0.305)	(0.262)	
P mg/g	0.47	0.45	0.41	1.29
	(0.0318)	(0.0245)	(0.0199)	
C/N	41.4[ab]	39.9[a]	45.7[b]	4.65*
	(1.30)	(0.916)	(1.81)	

*$p < 0.05$

5.4. Discussion

Organic matter inputs

The biomass was apparently the highest in mounds because of the existence of established buttressed trees, and was the lowest in gaps. Mass of litter fall is affected by the DBHs of surrounding trees (Ferrari and Sugita 1996). Also, in tropical peat swamp forests, decreasing litter fall mass was observed with declining basal area of trees at stand level (Brady 1997). The degree of flooding also affects the mass of litter fall. A plant responds to high frequency of flooding by increasing above-ground production (Megonigal and Day 1992). Because of the relatively higher elevation of mounds, the degree of flooding is the lowest on mounded sites. The results of the present study conflict with such a response of plants to flooding intensity (Figure 5-1). It appears that the biomass around the litter traps explains the difference and rank of litter fall mass among the three types of sites.

In the upper 20 cm soil, mounds had greater mean fine-root mass production than gaps (Figure 5-2). It appears that this difference in fine-root production simply reflects a difference in biomass around the ingrowth core. The biomass around the ingrowth core is the highest in mounds because of the existence of established buttressed trees, and the lowest in gaps. Root systems respond to disturbances with immediate and massive dieback. Subsequently, fine-root mass is rebuilt, but mass and production does not recover to pre-disturbance levels for several years (Vogt et al. 1981, Vogt et al. 1987, Fahey and Hughes, 1994). However, some studies did not detect such reduction of fine-root production (Ostertag 1998) (see Jones et al. 1996). Also, in this study, no significant difference in fine-root production between gaps and the understory was found.

Root biomass and production are often highest in well-aerated microsites and lowest in constantly anaerobic sites (Lieffers and Rothwell 1987, Megonigal and DAy 1992). The net

primary production is the highest on such aerated microsites. Root growth is also higher if surface flooding is rare (Montague and Day 1979, Powell and Day 1991, Burke and Chambers 2003) or periodic (Megonigal and Day 1992). Jones et al. (1996) reported that more aerated conditions were found in mounds than in flats in floodplain forests.

In this study, the difference and rank among the three types of sites in terms of fine-root production can be explained by degree of aeration. The lower bulk density of mounds also indicates the relatively aerated condition of mounds around the established buttressed trees. Moisture levels of surface soils in gaps are often greater than those under adjacent closed canopy (Vitousek and Denslow 1986, Uhl et al. 1988, Becker et al. 1988, Denslow et al. 1998). This is because reduction in fine root mass following tree fall reduces transpiration loads on gap soils and results in high moisture content (Denslow et al. 1998). It can be assumed that such effects of reduced transpiration loads in gaps protracts the gap soil water-saturation and such saturated soil possibly depresses the fine-root growth. Therefore, the effects of both the aerated condition and biomass contribute to explain the difference in fine-root production between mounds and gaps and the rank in fine-root production among the three types of sites.

According to Megonigal and Day (1992), there was a tendency for below-ground production of bald cypress saplings to be higher and above-ground production to be lower in periodically flooded trees than in continuously flooded trees. At the stand level, Brady (1997) reported that in tropical peat swamp forests of the Riau Archipelago, root ingrowth rates were increased along the gradient of increasing peat depth, while above-ground litter fall showed the opposite trend, and where the peat was deep, the water table dropped rapidly in the dry season. In the present study, the rank in terms of mass of litter fall and that of fine-root production among the three types of sites were the same, while the ratio between mean litter fall mass/ mean fine-root showed the opposite order (gaps > non-mounds > mounds), and the values were

14.1, 6.10, and 4.36, respectively. The differences in above- and below-ground production among microhabitat types are strongly affected by biomass rather than by hydrological regime.

Decay of leaf and wood litter

Litter decomposition is influenced by flooding. Some litterbag studies have shown greater mass loss in periodically flooded sites than in unflooded sites (Day 1982, 1983). Other researchers have found that decomposition is most influenced by moisture at low moisture contents during dry periods (Osborne and Macauley 1988, Cornejo et al. 1994). A hydrological regime such as the anoxic condition (Johnson and Damman 1991) and low pH (between 3.5 and 4.5 (Momose and Shimamura 2002)) (Benner et al. 1985) of tropical peat swamp forests may depress the decomposition process. However, in the present study, no explicit differences in leaf litter decomposition were found among the three types of sites (Figure 5-3). Frequency of flooding among the three types of sites were mounds < non-mounds ≈ gaps. Such effects of hydrological regime do not explain the lowest value of decomposition constant in gaps. Some studies have suggested that microbial activity and resulting decomposition rates are reduced in gaps (Zhang and Zak 1995, 1998). This effect in gaps is one possible explanation for the lowest decomposition constants occurring in those sites.

Wood decomposition is affected by hydrological regime (Harmon et al. 1986). The decomposition rate of *Palaquim burckii* wood block appeared to be affected by hydrological regime (Figure 5-4). The increasing depth from the peat surface inhibits decomposition of wood block of *Palaquim burckii*, while mounded sites showed the highest decomposition rate.

The decomposition rate of wood block in the mounded site was clearly higher than that of the ground level site, while that of leaf litter in mounded sites and non-mounded sites under the forest canopy were similar. One possible explanation for the difference in decomposition rate

between leaf litter and wood block is the underlying difference in mesh size between the leaf litter and wood block decomposition experiments. It must be noted that the mesh size for the decomposition experiment is larger than that of litterbags, and allowed macrofauna to enter. There was no explicit difference in decomposition rate of leaf litter between mounds and ground level sites (0 cm). Variance in decomposition constant was very high in mounds. This indicates that the results of the decomposition experiment in mounds were highly affected by chance. The possibility of the entry of macrofauna in wood blocks is higher on mounds than at ground level, given that macrofauna activity is depressed by flooding. However, Anderson et al. (1983) found no difference in leaf litter decay using fine and coarse mesh bags. Further studies are needed to determine the effect of macrofauna on the decomposition process in tropical peat swamp forests.

Litter and peat quality

According to Brady (1997), litter CO_2 emissions were positively correlated with N and P in tropical peat swamp forests. Several studies have demonstrated that litter decomposition rates are positively correlated with nutrient content and negatively correlated with litter quality. In tropical peat swamp forests, rates of litter decay were associated with initial N and P contents, and surface peat decay was correlated with C/N ratio (Brady 1997). In the present study, significant differences in chemical components of litter quality were shown in terms of N, Na, and C/N ratio (Table 5-3). The lowest concentration of N in litter fall of mounds raises the possibility that the litter fall on mounds has a relatively lower decomposition rate.

On the other hand, no differences in the C/N ratio of peat samples were shown among four habitats (Table 5-2). This indicates the possibility that the decomposition of the peat matrix is regulated by external factors such as hydrological regime. The degree of peat matrix decomposition was indicated by bulk density. The lower bulk density on mounds indicated a

relatively less decomposed peat matrix in mounded sites than in non-mounded sites.

5.5. Conclusion

The results of this chapter indicate that the regime of production and decomposition differed among mounded sites, non-mounded sites, and gaps. There was a significant effect of site on annual rates of litter fall for leaf, wood, and total materials. In terms of totals, for leaves and woods, the mean litter fall values were highest on mounded sites around established buttresses, and lowest in gaps. The rank in fine root production among the three types of sites was mounds around established living buttressed trees > ground level sites > gaps. Thus, the results of this study supported my first hypothesis that production is highest on mounds and lowest in gaps. The results of decomposition experiments of leaf litter and wood block did not show such a clear difference. The rank in decomposition rates of leaf litter among the three types of sites was ground level sites > mounds around established buttresses > gap sites. But no difference was observed between any of the pairs of treatments among the three treatments. The results of wood block decomposition showed that decomposition rates have a tendency to decrease as the depth from the peat surface increases. However, this study showed only a marginally significant difference in decomposition rates of wood block between mounds and non-mounds. Difference in the balance between production and decomposition is strongly affected by the production rather than the decomposition rate. In other words, the rate of above- and below-ground production strongly determines dynamic aspects, such as rising or sinking, of the peat surface. Thus, my third and fourth hypotheses were supported by the data. The production of mounded sites, which is the highest above- and below- ground, has the strongest effect on the rising peat surface, while the effect is weaker in gaps. Therefore, I conclude that rising and sinking of peat surface occurs along a temporal scale.

CHAPTER 6

General discussion

6.1. General discussion

Plant species coexistence and organic matter dynamics in tropical peat swamp forest

The result of the present study support my two general hypotheses that microtopographic heterogeneity of the peat surface provides an axis of habitat partitioning of plant species and that rising and sinking of the peat surface (elevation dynamics) occurs in the peat swamp forest. The lower input of above- and below-ground organic matter in gaps (Figure 5-1 and 5-2) and less elevated mounds of the dead established buttressed trees (Figure 4-1c,d), relative to that around the living established buttressed trees, indicates a role of gaps as a phase during which the modified peat surface (mounds) return to pre-modified status (non-mounded sites). On the other hand, establishment of huge buttressed trees means the creation of mounded sites. The establishment and death of huge buttressed trees cause the rise and sink of the peat surface, respectively, and result in an undulating peat surface. Sinking and creation of mounds affect plant distribution. Creation of mounds provides habitats for flood-intolerant species, and the death of established buttressed trees provides habitats for flood-tolerant species. Thus, plant species coexistence in the present forest can be explained in terms of kinetic equilibrium along spatio-temporal scale.

I propose a dynamic model that allows us to explain the mechanisms underlying the spatial patterns and to examine the probability of coexistence of tree species in the tropical peat swamp forest (Figure 6-1). The model is based on the following assumptions: (i) an establishment of a huge buttressed tree creates a mounded site around them; (ii) death of a huge buttressed trees indicates sink of a mounded sites; (iii) there are flooding-tolerant and –intolerant tree species;

and (iv) there are shade-tolerant and –intolerant tree species (Appendix 1).

I suggest that the forest is composed of areas that can be allocated to one of four phases based on the canopy type and microtopographic form; mounded sites under canopy in MU-phase, non-mounded sites undercanopy in NU-phase, mounded sites in a gap in MG-phase and non-mounded sites in a gap in NG-phase. In NG-phase, individuals of flooding-tolerant and shade-intolerant tree species like *Knema intermedia* dominate. Canopy gaps in tropical moist forests return to pre-gap phase within 5 years in tropical moist forest (Fraver et al. 1988, van der Meer 1997). This time scale is less than establishment of huge buttressed trees that forms mounded sites. Thus, whether regenerating tree species are mound-forming or non-mound-forming, NG-phase will replace NU-phase. In NU-phase, individuals of flooding-intolerant and shade-tolerant species dominate. If disturbance occurs NU-phase will replace NG-phase. *Shorea teysmanniana* is one of the mound-forming tree species that can inhabit in non-mounded sites (Appendix 2). Once such a huge individual of mound-forming tree species like *Shorea teysmanniana* is established, this phase will replace MU-phase. In MU-phase, individuals of flooding-intolerant and shade-tolerant species dominate. If disturbance occurs in MU-phase, this phase will replace MG-phase. In MG-phase, mound will sink because above- and below-ground productions decrease. Thus, this phase will replace NU- or NG-phases.

The model suggests that plant species coexistence in tropical peat swamp forests is facilitated by plant interaction via soil process, and effects of habitat modification of large plants are important. The model also clearly showed individualistic establishment and death have strong effects on plant community, and its death and establishment have different effects.

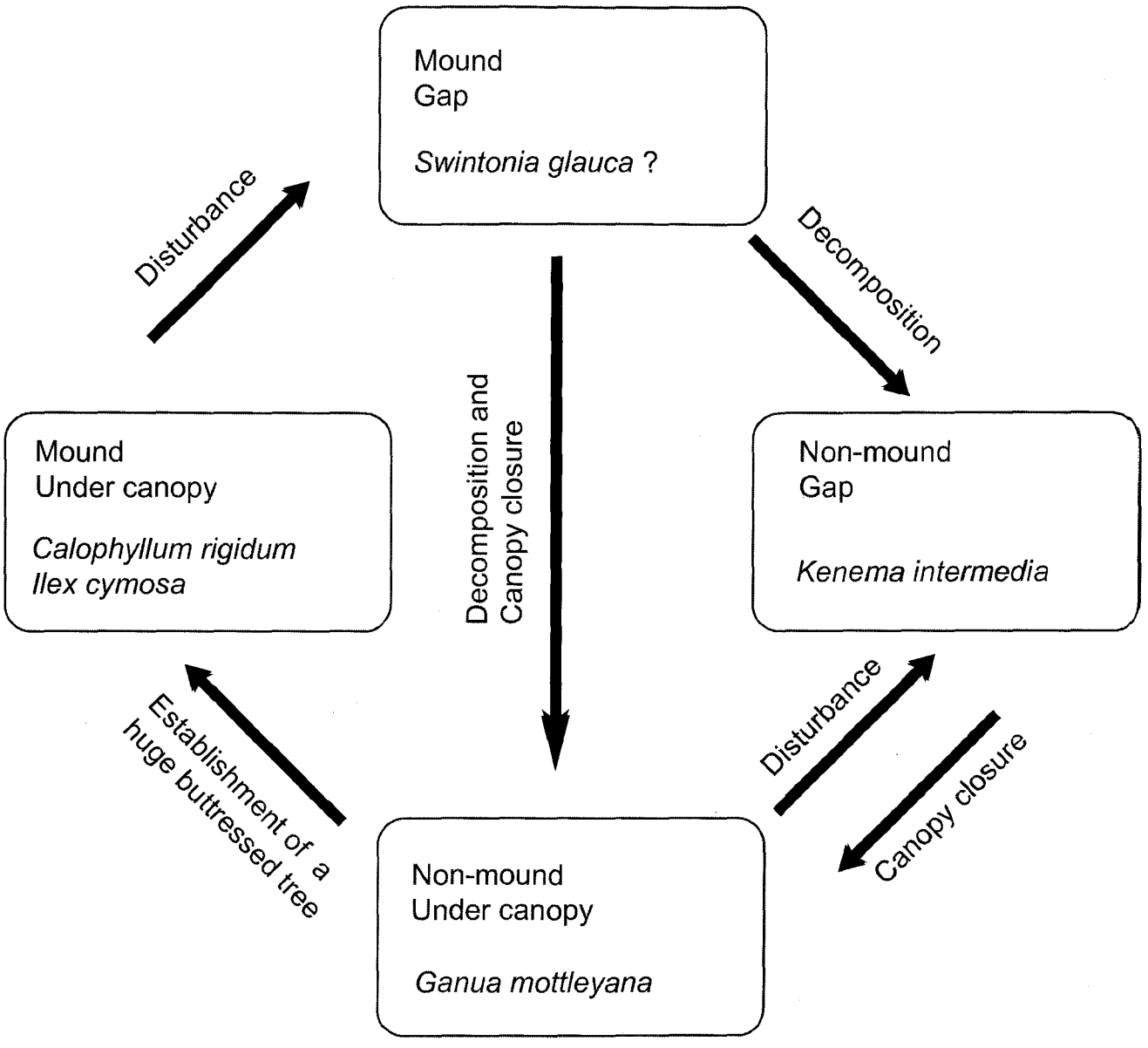

Figure 6-1. Diagram of four phase dynamics used to explain plant species coexistence in the tropical peat swamp forest. Plant species in frames are dominant or regenerating plant species in each phase.

6.2. Implications

Ecological implications

Because elevation dynamics explains plant species coexistence in terms of kinetic equilibrium and strongly relates to organic matter dynamics, elevation dynamics is similar to hummock-hollow cycles (Tallis 1983) in boreal peat lands. In boreal peat lands, rapid upward growth of the ground surface during hummock-building results in progressively increasing dryness of the surface layers, and the ultimate establishment of communities with negligible peat accumulation. Cessation of hummock growth is accompanied by rapid upward growth in intervening hollow areas, and the water table is gradually raised as Sphagnum moss accumulates. Then the degenerating hummocks become waterlogged and are converted into hollows. However, hummock-hollow cycles are unlikely to occur in boreal peat lands (Svensson 1988, Weltzin et al. 2001), even on a time scale of 60 years (Backéus 1972).

It is obvious that the rate of decomposition and production is higher in tropical peat land than in boreal peat lands. Mounds in tropical peat swamp forests are maintained by root structures around large buttressed trees, and contain spaces not filled with peat (Yonebayashi et al. 1997), whereas the mounds in boreal peat are maintained by the accumulation of bryophytes for many generations. The time scale of habitat cycles is the same as the longevity of plant individuals in the former, whereas the time scale of habitat cycles is much longer than life cycles of ramets in the latter. In this manner, the elevation dynamics of mounds in a tropical peat swamp forest differs from the hummock-hollow dynamics of mounds in boreal peat lands.

In wetlands, the stability and permanence of microsites strongly influence survivorships of tree seedlings (Huennecke & Sharitz 1986) and plant distribution (Keddy 1983, Denneler et al. 1999, Castelli et al. 2000). In peat swamp forests, gaps resulting from the death of mature buttressed trees are examples of impermanent microsites. The mounded sites around living

mature buttresses were of significantly higher elevation than those around dead mature buttresses. This indicates that mounded sites around decaying buttresses are sinking. The ground surface in such gaps is often inundated in rainy seasons, and inundations have negative effects on flood-intolerant species.

In addition to the impermanence of microtopography in gaps, high light levels are also impermanent. Fraver et al. (1988) documented that light levels in gaps return to pre-gap levels by 48 months in Panamanian tropical moist forest, and van der Meer (1997) found that canopy gaps in French Guiana close 5-6 years after creation. If such canopy closure occurs, surviving seedlings are left in the understory, and the diminished light environment decreases the survival of seedlings of light-demanding species.

Thus, the relative permanence of mounds in non-gaps and the impermanence of mounds in gaps are characteristic of the tropical peat swamp forest. These characteristics of the forests have important implications in gap dynamics, which is a well-known hypothesis to explain plant species coexistence (Augspurger 1984a, Martìnez-Ramos et al. 1988, Whitmore 1989). The creation of gaps produces heterogeneity of light conditions. Tree species perform differently under various light conditions. In the gap dynamics, disturbance is more preferable for light-demanding (stress-intolerant) species, whereas it is a less favorable event for shade-tolerant (stress-tolerant) species. Like elevation dynamics, gap dynamics is based on a habitat-partitioning hypothesis.

Here, the relative permanence of mounds in non-gaps and the impermanence of mounds in gaps modify the effect of gap dynamics. Disturbances cause the disappearance of mounds, which, from a viewpoint of elevation dynamics, are suitable habitats for stress-intolerant species, whereas, from a viewpoint of gap dynamics, such disturbances provide habitats for stress-intolerant species.

This study provided evidence that specific plant groups produce subtle differences through above- and below-ground production at the peat surface in tropical peat swamp forests. Such functional effects became clear when the species were classified into categories and compared according to their functional type (i.e., buttressed trees vs. trees with pneumatophoreses, such as *Stemonurus secundiflorus* and *Ganua mottleyana*). Thus, grouping species into associated microtopographic form and size classes in the forest affords an adequate and useful representation of their effects on organic matter dynamics. Grouping by root system and size class indicates their specific regime of production and decomposition of organic matter. Further, this study makes it possible to provide useful implications by focusing on individualistic performance such as the establishment, mortality, and life cycle of specific functional trees.

The highest above- and below-ground production of huge trees may be common to other tropical rain forests in which there are huge trees that reach the emergent canopy. Burghouts et al. (1998) reported that the most important factor determining spatial heterogeneity of organic matter and element dynamics on the forest floor is the site-specific amount of leaf litter fall rather than spatially variable decomposition rates. The large amount of litter fall around emergent trees revealed in the present study can produce patches where large amounts of litter inputs to the soil can be observed. Consequently, such patches may result in a specific chemical and physical properties of the soil, and emergent trees may be used as an index of such soil properties.

Effects of habitat modification have often been documented in harsh sites such as salt marshes (Callaway 1994, Bruno and Kennedy 2000), arctic regions (Walker and Chapin 1986), semi-arid environments (Pugnaire et al. 1996, Tirado and Pugnaire 2003), and deserts (Franco and Novel 1989, Forseth et al. 2001), because such environmental modification is more important for plants under relatively high environmental stress (Pugnaire and Luque 2001).

Modifications of habitats are conducted by functions of the canopy or changes in litter quality. The presence of the canopy provides a modified thermal condition in an arid or semi-arid environment and protects the below-canopy plants from predation (Rousset and Lepart 2000) or heavy snow pressure (Carlsson and Callaghan 1996). Aggregated litter fall produces islands of fertility in arid environments. Highly concentrated nutrients in the litter fall of specific plants such as leguminous plants (Pugnaire et al. 1996) and hemi-parasites (Quested et al. 2003) improve the nutritive condition of the soil. Tropical peat is characterized by low nutrient content and high acidity, and results in a harsh environment. In the tropical peat swamp forest, the effect of habitat modification is as marked as that in other harsh environments. The present study provides the first evidence that plant-plant interaction occurs in a tropical swamp forest, and organic matter dynamics on an individualistic plant scale has an effect of habitat modification.

Implications for ecology of tropical peat swamp forests

In the tropics, peatlands are distributed in East and South-East Asia, Africa, the Caribbean, and Central and South America. The Malay archipelago contains the largest area of peatland in the tropical zone. Most of such peatlands are located at low altitude in the coastal and subcoastal lowlands of New Guinea, Borneo, and Sumatra. The total area of undeveloped tropical peat is estimated to be between 20 and 45 million hectares, which represents approximately 12% of the global peat land resource (Immirzi and Maltby 1992, Lappalainen 1996 (cited in Page et al. 1999)).). Tropical peat swamp forests in South-East Asia are well known to show a catenary sequence of vegetation along the gradient of peat depth in Sarawak and Burnei (Anderson 1961), Kalimantan (Page et al. 1999), and Sumatra (Brady 1997, Momose and Shimamura 2002).

Though peat thickness cannot influence vegetation directly, differences in many aspects of peat characteristics have been associated with peat depth, and contribute to explain the catenary

sequence of vegetation directly. Such differences in peat characteristics among vegetation types can be seen in their chemical, physical, and hydrological features and in organic matter dynamics (Brady 1997, Page et al. 1999, Momose and Shimamura 2002).

Previous studies that focused on the plant community and peat properties were comparative studies among catenary sequences of vegetative zonation. Some recent studies have dealt with internal mechanisms within a stand of tropical peat swamp forest. Garvin and Peart (1997) studied the population dynamics of *Tetramerista glabra* Miq., which is also one of the dominant species in the study forest; Nishimura and Suzuki (2001) studied the morphological features of tree seedlings; and Miyamoto et al. (2003) described the spatial associations between tree species and peat depth. The results of the present study contribute to explain plant species coexistence and underlying mechanisms in tropical peat swamp forests. In other words, previous studies have dealt with plant species coexistence relative to the catenary sequence of vegetation. On the other hand, this study dealt with plant species coexistence within a stand of tropical peat swamp forest.

Implications for conservation of tropical peat swamp forests

Wyatt-Smith (1959) and Anderson (1983) have shown that the peat swamp forests in Southeast Asia are a valuable timber resource. Forestry is likely to be the most sustainable use of tropical peat swamp forests (Brady 1997, Yamada 1997). This study revealed the maintenance system of plant species coexistence in tropical peat swamp forests. The maintenance system is based on interactions between plants and peat. Based on the findings of this basic study, sustainable forest management that takes in account the maintenance system can be developed.

For example, forest harvesting cuts mainly large individuals. Harvesting of huge individuals

causes a drastic loss in the amount of organic matter inputs. Of harvested species, many huge buttressed individuals are included. Thus, harvesting of huge trees leads to loss of microtopographic heterogeneity. Harvesting methods that preserve not only microtopographic heterogeneity but also the dynamic aspects of microtopography are essential in order to use peat swamp forests in sustainable ways.

6.3. Conclusion

In chapter 3, the survival and growth of seedlings of *Swintonia glauca* and *Stemonurus scorpioides* are affected by both light conditions and elevation. Survival and growth responses of seedlings of *Swintonia glauca* were stress-intolerant to flooding and light conditions, while the responses of seedlings of *Stemonurus scorpioides* showed comparatively higher stress-tolerance. Elevation affects the establishment of seedlings of stress-intolerant species like *S. glauca*, though the effects of light conditions and density mortality were found to be stronger than that of elevation. On the other hand, lower elevation positively affects the establishment of seedlings of stress-tolerant species like *Stemonurus scorpioides*. For seedlings of *S. scorpioides*, neither density- nor distance-dependent mortality was found, and there was no positive effect of light conditions. Thus, chapter 3 revealed that the importance of elevation for seedling establishment relative to other abiotic and biotic environmental conditions is different according to the degree of stress-tolerance of seedlings.

Chapter 4 revealed that plant distribution is affected by microtopographic heterogeneity associated with their degree of flood-tolerance. The spatial point pattern analyses indicate that *Calophyllum rigidum* and *Ilex cymosa* trees are flooding-intolerant, whereas *Knema intermedia*, *Eugenia lepidocarpa* and *Tetractomia tetlandra* trees are flood-tolerant. The results of this study support my hypothesis that the spatial distribution pattern is the consequence of a

microtopographic interaction associated with the established buttressed and/or non-mound-forming trees, and microtopographies contribute to species coexistence in this forest. Thus, spatial heterogeneity of the microtopographic form provides an axis of habitat partitioning in the tropical peat swamp forest.

Results in chapter 5 indicate that the regime of production and decomposition differed among mounded sites, non-mounded sites, and gaps. A significant effect of site on annual rates of litter fall for leaf, wood, and total materials was observed. In terms of totals, including leaves and woods, the mean litter fall was highest on mounded sites around established buttresses, and lowest in gaps. The rank in fine root production among the three types of sites was mounds around established living buttressed trees > ground level sites > gaps. Thus, the results of this study supported my first hypothesis that production is the highest on mounds and the lowest in gaps. The results of decomposition experiments of leaf litter and wood block did not show such a clear difference. The rank in decomposition rates (k) of leaf litter among the three types of sites was ground level sites > mounds around established buttresses > gap sites. But no significant difference was found between any of the pairs of the three treatments. Results of wood block decomposition showed that decomposition rates have a tendency to decrease as depth from the peat surface increases. However, only a marginally significant difference in decomposition rates of wood block was found between mounds and non-mounds. In contrast to results of production, results of decomposition rates did not show clear a difference between mounded sites and non-mounded sites. The difference in the balance between production and decomposition is strongly affected by rate of production rather than by the rate of decomposition. In other words, the rate of above- and below-ground production strongly determines dynamic aspects, such as rising and sinking, of the peat surface. The highest above- and below- ground production of mounded sites has the strongest effect on causing rises in the

peat surface, while the effect is weaker in gaps. Findings in this study revealed that the process of rising and sinking of peat surface occurs along a temporal scale.

In conclusion, there is microtopographic heterogeneity in the tropical peat swamp forest. The microtopographic heterogeneity contributes to species coexistence by providing an axis of habitat differentiation, and is controlled by plant activity through organic matter dynamics. The establishment and death of huge buttressed trees results in rising and sinking of the peat surface (elevation dynamics), respectively. Thus, microtopographic heterogeneity is maintained along a temporal scale. Based on the habitat partitioning hypothesis, microtopographic heterogeneity contributes to plant species coexistence. In the elevation dynamics, the disappearance of a mounded site augurs the creation of a habitat for flood-tolerant species; by contrast, the rise of a mounded site augurs the creation of a habitat for flood-intolerant species.

The elevation dynamics has several important implications. First, the dynamics modifies the effect of gap dynamics as a result of the changes in microtopography that occur in gaps. Second, because rises and sinks of the peat surface are associated with plant activities, the dynamics is an example of habitat modification of tree species. The f]indings of this dynamics constitutes the first observation of a demonstrated effect of habitat modification in tropical swamp forests. Third, because a large amount of production of huge trees is common to other tropical rain forests and the organic matter element dynamics on the forest floor is affected by the amount of litter input, similar effects of huge trees may be considered to occur in other tropical forests, widening the applicability of the findings presented herein.

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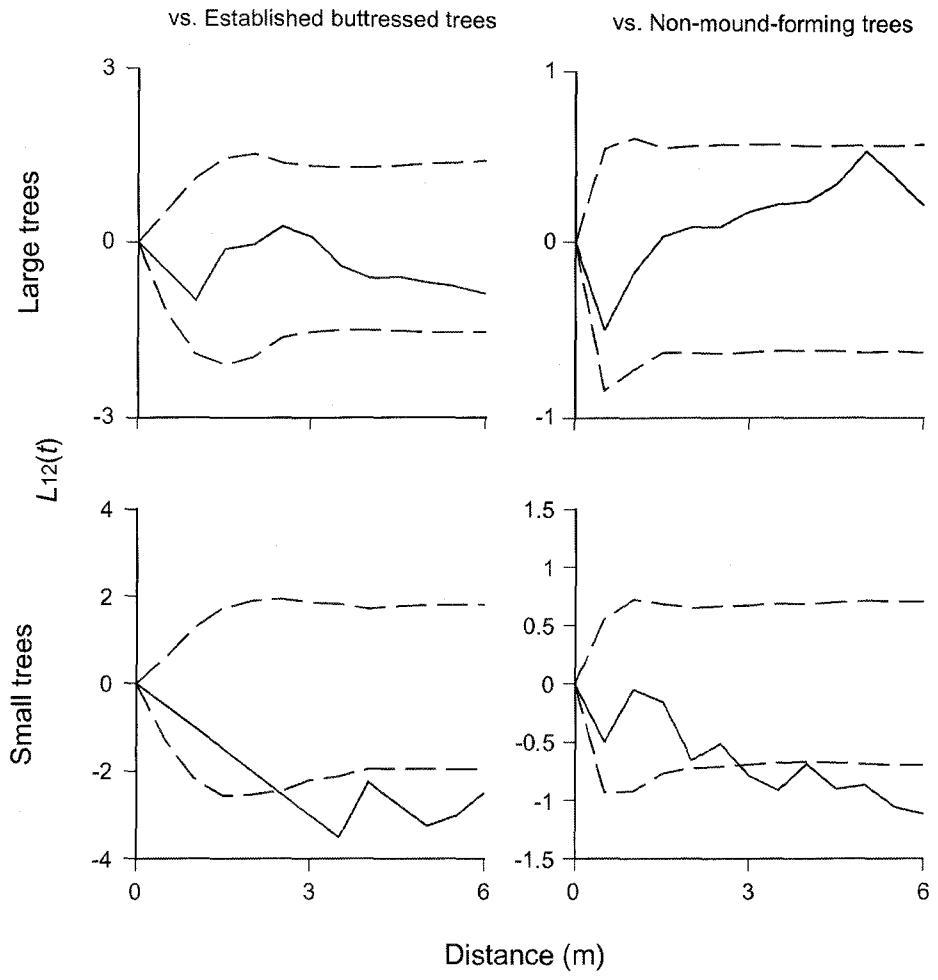
Appendix 1

I selected ten gaps to examine the association between the abundance of the top ten species and in individual number and canopy gaps in and around the study plot (Chapter 4). I regarded each gap as an ellipse and recorded the lengths of the longest and shortest axes. Along each long axis, I laid out 2 m wide transects. I measured DBHs of all individuals found within the transects. The total area of the gap transects were 380.8 m^2. Followings are individual number of the top 10 species in the 1.0 ha study plot (Chapter 4) and in the transects. Data for *Shorea teysmanniana* is added. Chi-square tests were performed to test whether distribution of each species were independent of the distribution of total trees. The results of the tests indicate that there were less individuals of *Ganua mottleyana* and *Ilex cymosa* in the gaps, while less individuals of *Knema intermedia* in the 1ha plot.

Species	1ha plot	Gap transect	χ^2
Ganua mottleyana	1212	29	5.9*
Stemonurus secundiflorus	566	18	0.59
Syzigium rhizophorum	532	22	0.18
Calophyllum rigidum	484	18	0.11
Ilex pleiobrachiata	462	16	0.16
Knema intermedia	280	20	7.0**
Tetractomia tetrandra	279	17	3.3
Swintonia glauca	244	4	2.4
Syzigium lepidocarpum	238	7	0.48
Ilex cymosa	231	2	4.5*
Shorea teysmanniana	189	10	0.95
Total	7941	260	

*$p < 0.05$



Appendix 2.

$L_{12}(t)$ values of bivariate spatial associations of *Shorea teysmanniana* trees versus established buttressed trees versus two plant groups (established buttressed trees (dbh ≥ 40 cm) and non-mound-forming trees (dbh ≥ 15 cm)). The solid line shows observed $L_{12}(t)$ value, broken lines show the 95 % confidence envelopes for the pattern expected from an independent distribution.